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ORIGINAL ARTICLE

Morphometric divergence and allometric growth reveal phenotypic stock structure in *Wallago attu* across three barrages of the Indus River, Pakistan

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Abstract
Wallago attu (Bloch & Schneider, 1801), an economically valuable silurid catfish species, is extensively harvested from South Asian river systems. However, information on stock levels in the Indus River population in Pakistan remains limited. This study examined morphological differences among three geographically distinct populations of *W. attu* from the Chashma, Sukkur, and Taunsa Barrages, located at different elevations in the Indus River system. Thirty-four morphometric characters were recorded from 75 individuals (25 per location) using a landmark method, and multivariate, univariate, and allometric analyses were conducted. Multivariate analysis of variance showed significant differentiation in body shape among the three *W. attu* populations (Pillai's trace= 1.49, $F_{(26, 122)}$= 13.80, P<0.001). Thirteen of the 34 characters showed significant differences after False Discovery Rate correction, while total, fork, and standard lengths showed no significant differences among the three populations, meaning there were no significant differences in size among the three populations. However, they showed significant differences in body proportions, specifically head region and fin traits, such as post-orbital length (η^2= 0.31) and head depth (η^2= 0.25). Principal component analysis showed size-based overlap along the first axis (53.2%) but partial segregation along shape axes, with the Chashma group as the most distinct cluster. Cross-validated discriminant analysis classified 84% of individuals to their sites of origin. Allometric growth was isometric in the Sukkur and Taunsa Barrage samples. In contrast, non-isometry was common among the Chashma fish, and the length-weight relation showed negative allometry in the Chashma and Sukkur samples and isometry at the Taunsa Barrage. This study shows that the three barrage samples represent morphologically distinct phenotypic stocks, most likely influenced by differences between lentic and lotic habitats in the Indus River.

Keywords: *Wallago attu*, Morphometrics, Allometric growth, Phenotypic stock, Indus River, Population divergence

INTRODUCTION

Freshwater fishes represent a significant part of global biodiversity and the basis of the food security and livelihoods of millions of people (Muhammad et al. 2023), but they are some of the most endangered vertebrates because of overfishing (Ali et al. 2024; Muhammad et al. 2024), environmental destruction, pollution, invasive species (Muhammad & Zain-ul-Abideen 2022), and changes in hydrology (Grill et al. 2019). For sustainable management and conservation of exploited fishes, knowledge about their population or stock structure is essential because a species is usually made up of multiple self-sustaining sub-populations that vary in growth, condition, and productivity and need to be managed separately to avoid depletion (Begg & Waldman 1999; Cadrin 2000; Rawat et al. 2017). Therefore, understanding this structure is necessary before developing conservation and fisheries management plans.

Among the techniques used to discriminate between stocks, morphometric studies are relatively easy to use and highly informative. Morphometric traits reflect the combined influences of genotype and the environment in which the organism developed, and morphometric analysis thus helps identify phenotypic stocks, i.e., stocks that vary in morphology regardless of genetic distance (Cadrin 2000; Rawat et al. 2017). The landmarks approach and the truss network, in which corresponding points on the body are recorded and distances measured and subjected to

multivariate analysis such as principal component and discriminant analysis, effectively capture shape changes and place minimal constraints on the direction of change (Strauss & Bookstein 1982; Klingenberg 2022). Because this technique is fast and inexpensive compared with other approaches, it has proven successful in discriminating between populations of different fish species in both freshwater and marine environments (Turan 2004; Rawat et al. 2017; Kwikiriza et al. 2023).

Stock identification using morphometrics relies on the known plasticity of fish bodies. Fish morphology varies greatly according to the environment and hydrology, such as water velocity, temperature, resource availability, and predation, such that fish living in various environments often vary in body and head morphology (Langerhans 2008; Langerhans & Reznick 2010; Franssen 2011; Kelley et al. 2017; Secer et al. 2022; Hetzel & Forsythe 2023). Head region characters, which have functional relevance for feeding, respiration, and sensory perception, in addition to body depth and fin size characters, are some of the characters that show high responsiveness to the environment and consistently feature as the major discriminants in population-level studies (Kelley et al. 2017; Kumar et al. 2023). Because of this environmentally induced variability, morphometrics is a useful tool for studying population substructure in riverine fishes that inhabit environmentally diverse and fragmented habitats.

Wallago attu (Bloch & Schneider, 1801), also known as the Asian sheatfish or freshwater shark, is a large predatory catfish of the Siluridae family, native to the freshwater environments of South and Southeast Asia, which include Pakistan, India, Bangladesh, Nepal, Sri Lanka, as well as most of mainland Southeast Asia (Talwar & Jhingran 1991; Sherzada et al. 2024). This demersal and potamodromous catfish lives in rivers, floodplains, lakes, and reservoirs and is a major predator in these ecosystems (Ng et al. 2019). *Wallago attu* is economically and nutritionally important and is highly sought after for its food value because of its fast growth, flesh quality, and low bone content, making it an attractive aquaculture candidate (Sherzada et al. 2024). Despite this, the number of *W. attu* individuals has decreased sharply. The IUCN Red List includes this species as vulnerable due to a suspected population decline of at least 30% over the last three generations, driven by over-exploitation, pollution, and habitat loss (Ng et al. 2019). Molecular research shows significant genetic diversity, along with signs of population bottlenecks, in riverine populations of this species (Sherzada et al. 2024; Kumar et al. 2024).

In Pakistan, *W. attu* is an essential constituent of the fish fauna of the Indus River system, which is fragmented by the construction of multiple barrages that control flow and create extensive reservoirs (Kalsoom et al. 2021). These structures alter local hydrology and limit the migration of potamodromous fishes, creating environmental heterogeneity and some isolation that may drive population divergence. However, despite the examination of the morphological variations of *W. attu* within the Indian river systems (Kumar et al. 2023) and studies on the genetic structure of the species in different regions, including the River Indus (Sajjad et al. 2023; Sherzada et al. 2024; Kumar et al. 2024), similar morphological analyses have not yet been performed for the Indus River system of Pakistan.

Few studies have examined spatial variation in morphometric characteristics among populations living in different parts of the Indus River. The majority of previous research on fishes in Pakistan has focused on species diversity (Imran et al. 2025; Sohail et al. 2025), distribution (Altaf 2026; Muhammad et al. 2026), feeding ecology (Shabir et al. 2025; Osmany et al. 2026; Zohra et al. 2026), and general biological traits. Although phenotypic diversity in *W. attu* is still poorly understood, morphological variation is an important indicator of population control, stock composition, and environmental adaptation. Therefore, the current study was carried out to investigate the morphometric variation in *W. attu* from three different locations on the Indus River, namely, Chashma, Sukkur, and Taunsa Barrages, representing a very clear downstream environmental gradient. More precisely, the aims of the current study are: (i)

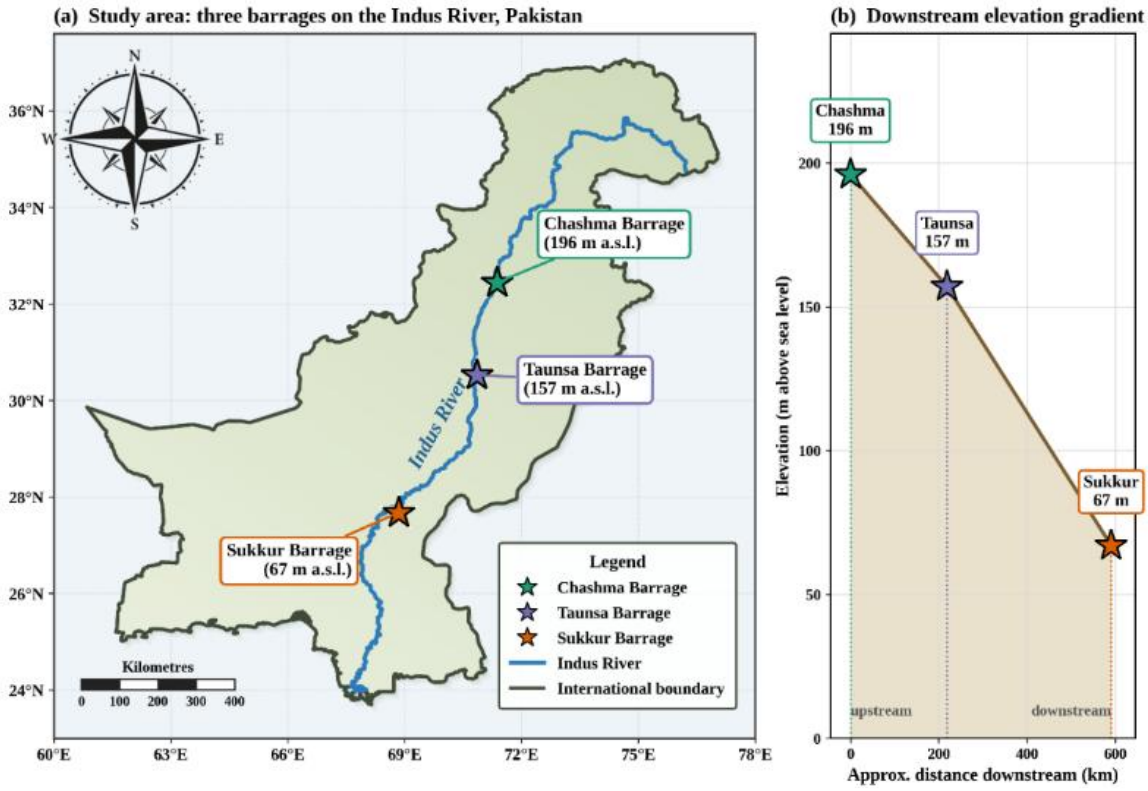


Fig.1. Location of the three sampling sites on the Indus River, Pakistan. (a) The Chashma, Sukkur, and Taunsa Barrages along the main stem of the Indus, with the river shown in blue and each barrage's approximate elevation above sea level indicated. (b) Longitudinal elevation profile illustrating the downstream gradient from Chashma (~196m) through Taunsa (~157m) to Sukkur (~67m).

to measure and compare 34 morphometric variables between the three populations, (ii) to identify those morphometric variables that distinguish them from each other, (iii) to examine allometric growth patterns, and (iv) to determine whether or not the three populations are morphologically distinct phenotypic stocks. The baseline information generated will support catfish conservation.

MATERIALS AND METHODS

Study area and sampling: The study was carried out using freshwater catfish *W. attu* were sampled at three barrages on the main stream of the River Indus in Pakistan: the Chashma Barrage (32.44°N, 71.37°E), the Taunsa Barrage (30.52°N, 70.86°E) and the Sukkur Barrage (27.67°N, 68.85°E). The three localities are distributed downstream along the river gradient, at about 196m above sea level at Chashma, 157m at Taunsa, and 67m at Sukkur, and are located several hundred kilometers apart along the river; their positions are marked in Figure 1. A total of 75 specimens (25 from each barrage) were collected from January to April 2025 as commercial fishing catch by local fishermen using cast nets and fishing nets. The collected fish were immediately placed on ice and sent to the Ecology and Evolutionary Biology Laboratory, Institute of Zoology, University of the Punjab, Lahore.

Specimen processing and identification: In the laboratory, each sample was washed with distilled water, dried with a soft cloth, and weighed on a digital balance (accurate to 0.01g). Species identification was done using appropriate taxonomic keys for inland fishes from the area (Mirza & Sandhu 2007; Talwar & Jhingran 1991). Each sample was coded to maintain proper records during the experiment, then photographed in lateral view on a measuring board with a scale bar, with the camera held perpendicular to the specimen.

Landmark-based morphometric measurements: The morphometric data were derived from the images using the landmark method. In this regard, the scaling parameter was defined using the scale bar in each image to ensure all measurements are presented in

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Table 1. Descriptive statistics (mean±standard deviation) of 34 morphometric characters of *Wallago attu* from the Chashma, Sukkur and Taunsa Barrages (n= 25 per site). All measurements are in centimeters except body weight (BW), which is in grams.

Character	Chashma Barrage (Mean±SD)	Sukkur Barrage (Mean±SD)	Taunsa Barrage (Mean±SD)
TL	30.98±2.96	31.57±5.30	33.05±2.42
FL	28.46±3.73	29.38±4.75	30.70±2.05
SL	27.21±3.54	28.35±4.81	29.66±2.05
PrDL	8.23±1.24	7.81±1.98	9.09±0.85
DFL	2.80±0.70	2.82±0.60	3.37±0.27
PrPecL	4.89±0.82	5.49±1.28	6.01±0.56
PecFL	4.13±0.25	3.87±0.65	4.24±0.33
PrPL	8.52±1.65	9.55±1.82	9.22±1.33
PFL	1.24±0.57	1.67±0.31	1.66±0.23
PrAL	11.64±2.53	11.76±2.52	13.15±1.03
AFL	15.00±1.73	15.66±2.76	15.97±1.47
PrOL	1.40±0.4	1.67±0.27	1.75±0.20
ED	0.77±0.07	0.76±0.13	0.77±0.14
HL	3.88±1.11	4.59±0.89	4.98±0.65
PoOL	2.59±0.56	3.18±0.67	3.54±0.53
BD	5.61±0.4	5.08±0.88	5.52±0.59
CFL	3.29±0.82	3.19±0.57	3.43±0.68
BW	130.86±29.52	137.70±62.42	164.44±42.02
UJL	1.95±0.98	2.33±0.58	1.95±0.73
LJL	1.88±0.99	2.61±0.65	1.72±0.66
CPL	0.91±0.20	0.82±0.16	0.84±0.60
CPD	1.34±0.16	1.27±0.25	1.29±0.15
CH	2.06±1.10	1.70±0.92	1.68±0.37
HD	2.22±0.35	2.79±0.51	2.35±0.41
PeAD	3.04±1.11	2.10±0.71	3.23±1.84
PcAD	6.89±1.87	6.16±1.36	7.05±1.20
PcPeD	3.87±0.65	4.44±0.76	4.09±1.13
ACD	16.00±1.87	16.81±2.75	16.57±1.44
ADD	6.90±0.60	6.46±1.08	6.89±0.69
PcDD	4.88±0.32	4.26±1.05	4.68±0.56
PcCD	22.06±2.74	22.50±3.41	23.58±1.99
PeDD	5.48±0.54	5.38± .01	5.79±0.59
PeCD	19.03±1.98	18.62±3.01	19.97±2.24
CDD	19.34±2.20	21.10±3.18	20.70±1.78

centimeters, and an input file for TPS was created using tpsUtil; thereafter, homologous landmarks were digitized in each specimen using tpsDig2 (Rohlf 2015). The landmarks were defined according to the methodology outlined by Naseer et al. (2023). Based

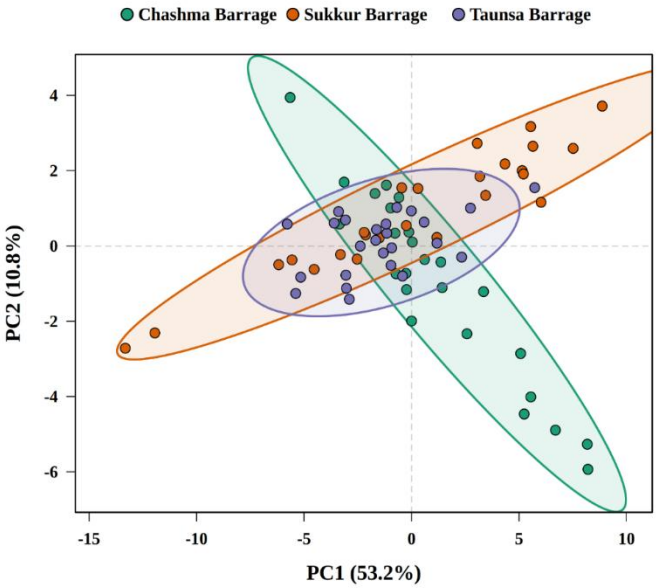


Fig.2. Principal component analysis of 34 morphometric characters of *Wallago attu* from the Chashma, Sukkur and Taunsa Barrages. Points represent individual specimens, and shaded polygons are 95% confidence ellipses for each site. PC1 (53.2%) is a general body-size axis, and PC2 (10.8%) is a shape axis.

on the resulting landmark coordinates, 34 morphometric characters were defined as inter-landmark distances (Table 1; Fig. 2), namely total length (TL), fork length (FL), standard length (SL), pre-dorsal length (PrDL), dorsal-fin length (DFL), pre-pectoral length (PrPecL), pectoral-fin length (PecFL), pre-pelvic length (PrPL), pelvic-fin length (PFL), pre-anal length (PrAL), anal-fin length (AFL), pre-orbital length (PrOL), eye diameter (ED), head length (HL), post-orbital length (PoOL), body depth (BD), caudal-fin length (CFL), upper-jaw length (UJL), lower-jaw length (LJL), caudal-peduncle length (CPL), caudal-peduncle depth (CPD), caudal height (CH), head depth (HD), and a series of fin-origin distances (PeAD, PcAD, PcPeD, ACD, ADD, PcDD, PcCD, PeDD, PeCD and CDD). Body weight (BW) was measured in grams. All measurements were done by one operator to eliminate inter-observer bias.

Statistical analysis: All analyses were conducted in R version 4.3. Statistical significance was defined at an alpha level of 0.05. Before analysis, the dataset was inspected for entry errors and biologically impossible data (such as instances where fork length exceeded

total length), which were then confirmed and corrected by comparing the entered data to the original photographs. Descriptive statistics (mean±SD) were calculated for all characters at each location.

Overall differences in body shape between the three groups were analyzed using one-way MANOVA. Since the number of morphological variables was larger than the within-group sample size, one-way MANOVA was carried out on the scores from principal components that explained ≥ 90% of the total variation in the dataset. Differences between individual characters were tested using one-way ANOVA, while partial eta squared (η^2) was used as the effect size measure. To correct the family-wise error from tests conducted on 34 characters, the resulting p-values were corrected according to the false-discovery rate method of Benjamini & Hochberg (1995), while those with an adjusted p-value of less than 0.05 were taken to be significant. In this regard, Tukey's honestly significant difference (HSD) post-hoc test was performed for the significant characters between all the sites. The principal component analysis (PCA) was conducted on the standardized characters.

To separate shape variability from size-related variability, each variable was log-transformed, and regression on the log-transformed total length was performed; the residuals from these regressions were treated as size-corrected shape variables (Reist 1985). The discrimination ability among these three populations was then calculated as the Mahalanobis distance of site centroids, while the assignment reliability was evaluated by linear discriminant analysis with leave-one-out cross-validation method.

The power function was used for determining the allometric growth of each of the characters as a function of total length. After logarithmic transformation, the model became a linear regression model of the form $\ln(Y)= \ln(a)+b\cdot\ln(TL)$, where the slope *b* indicates the allometric growth coefficient (Le Cren 1951). In the case of each character, the allometric coefficient *b*, along with the confidence intervals at the 95% level of significance and R^2, was determined, and the growth pattern was designated isometric, positively allometric, or negatively allometric based on the comparison with the isometric growth coefficient (*b*=1 for length-length relationship and *b*=3 for length-weight relationship).

RESULTS

Morphometric variation among sites: A total of 75 specimens (25 from each of the Chashma, Sukkur and Taunsa Barrages) were examined for 34 morphometric characters at the three barrages along the Indus River. The mean values and standard deviations of each character for the three sites are presented in Table 1. The three populations were broadly similar in overall body size: mean total length ranged from 30.98±2.96cm at Chashma Barrage to 33.05±2.42cm at Taunsa Barrage, with Sukkur Barrage intermediate (31.57±5.30cm), and mean body weight was highest at Taunsa Barrage (164.44±42.02g).

The results revealed highly significant overall differences in body form among the three populations (Pillai's trace = 1.49, $F_{(26,122)}$= 13.80, P<0.001). Univariate one-way ANOVAs with false-discovery-rate (FDR) correction identified 13 of the 34 characters as significantly different among sites (FDR-adjusted P<0.05; Table 2). Notably, the three gross size measures total length, fork length and standard length did not differ significantly among sites (FDR-adjusted P>0.05), indicating that the populations were comparable in overall size and that the differences lay in body proportions. The significant differences were concentrated in head-region and fin characters, the strongest being post-orbital length (PoOL; η^2= 0.31), head depth (HD; η^2= 0.25), pre-orbital length (PrOL), head length (HL), pelvic fin length (PFL), lower jaw length (LJL), pre-pectoral length (PrPecL) and dorsal fin length (DFL). Tukey HSD post-hoc comparisons showed that most of these differences separated Chashma Barrage from the other two sites (Table 2).

Principal component analysis summarised the multivariate variation (Fig. 2). The first principal component accounted for 53.2% of the total variance and represented a general body-size axis, while the

Table 2. One-way ANOVA and Tukey HSD post-hoc results for 34 morphometric characters of *Wallago attu* among the three sites. Significance codes are based on FDR-adjusted p-values: *** $P< 0.001$, ** $P< 0.01$, * $P< 0.05$, ns= not significant. η^2= partial eta squared (effect size).

Character	F	df	*P*	*P* (FDR)	η^2	Sig.	Pairwise differences (Tukey, $P<0.05$)
TL	1.98	2.72	0.146	0.186	0.052	ns	none
FL	2.32	2.72	0.105	0.163	0.061	ns	none
SL	2.82	2.72	0.066	0.132	0.073	ns	none
PrDL	5.19	2.72	0.008	0.027	0.126	*	Taunsa-Sukkur
DFL	8.44	2.72	<0.001	0.002	0.190	**	Taunsa-Chashma; Taunsa-Sukkur
PrPecL	9.10	2.72	<0.001	0.001	0.202	**	Taunsa-Chashma
PecFL	4.53	2.72	0.014	0.037	0.112	*	Taunsa-Sukkur
PrPL	2.67	2.72	0.076	0.136	0.069	ns	none
PFL	9.38	2.72	<0.001	0.001	0.207	**	Sukkur-Chashma; Taunsa-Chashma
PrAL	3.81	2.72	0.027	0.065	0.096	ns	Taunsa-Chashma
AFL	1.46	2.72	0.238	0.279	0.039	ns	none
PrOL	9.60	2.72	<0.001	0.001	0.211	**	Sukkur-Chashma; Taunsa-Chashma
ED	0.01	2.72	0.994	0.994	0.000	ns	none
HL	9.51	2.72	<0.001	0.001	0.209	**	Sukkur-Chashma; Taunsa-Chashma
PoOL	16.42	2.72	<0.001	<0.001	0.313	***	Sukkur-Chashma; Taunsa-Chashma
BD	4.63	2.72	0.013	0.036	0.114	*	Sukkur-Chashma
CFL	0.75	2.72	0.476	0.506	0.020	ns	none
BW	3.62	2.72	0.032	0.072	0.091	ns	Taunsa-Chashma
UJL	1.97	2.72	0.147	0.186	0.052	ns	none
LJL	9.22	2.72	<0.001	0.001	0.204	**	Sukkur-Chashma; Taunsa-Sukkur
CPL	0.39	2.72	0.677	0.698	0.011	ns	none
CPD	1.02	2.72	0.366	0.413	0.028	ns	none
CH	1.59	2.72	0.211	0.256	0.042	ns	none
HD	12.29	2.72	<0.001	<0.001	0.254	***	Sukkur-Chashma; Taunsa-Sukkur
PeAD	5.32	2.72	0.007	0.026	0.129	*	Sukkur-Chashma; Taunsa-Sukkur
PcAD	2.48	2.72	0.091	0.155	0.064	ns	none
PcPeD	2.75	2.72	0.071	0.134	0.071	ns	none
ACD	0.99	2.72	0.376	0.413	0.027	ns	none
ADD	2.36	2.72	0.102	0.163	0.061	ns	none
PcDD	4.95	2.72	0.010	0.030	0.121	*	Sukkur-Chashma
PcCD	1.98	2.72	0.145	0.186	0.052	ns	none
PeDD	2.13	2.72	0.127	0.186	0.056	ns	none
PeCD	2.00	2.72	0.142	0.186	0.053	ns	none
CDD	3.49	2.72	0.036	0.076	0.088	ns	Sukkur-Chashma

second component (10.8%) captured shape variation. Consistent with the ANOVA, the three sites overlapped along the size-dominated first axis but separated on the shape axes, with Chashma Barrage forming the most distinct cluster. Site-related differences in the individual significant characters are illustrated in Figure 3.

The distinctiveness of the three populations was quantified from the size-corrected shape variables. Chashma Barrage was the most distinct population, showing the largest summed multivariate (Mahalanobis) distance to the other two sites; the Chashma–Sukkur and Chashma–Taunsa distances (4.83 and 3.46, respectively) both exceeded the Sukkur–Taunsa distance (2.70), indicating that the Sukkur and Taunsa populations most closely resembled each other. A cross-validated linear discriminant analysis classified 84% of specimens to their correct site, with Chashma Barrage separated almost perfectly (22 of 25 specimens correctly assigned) and the few misclassifications occurring between the Sukkur and Taunsa populations.

Allometric growth was assessed by regressing the natural logarithm of each character on the natural logarithm of total length; the allometric coefficient (b) was compared with the isometric expectation of $b= 1$ for length–length relationships and $b= 3$ for the length–weight relationship (Table 3). At the Sukkur

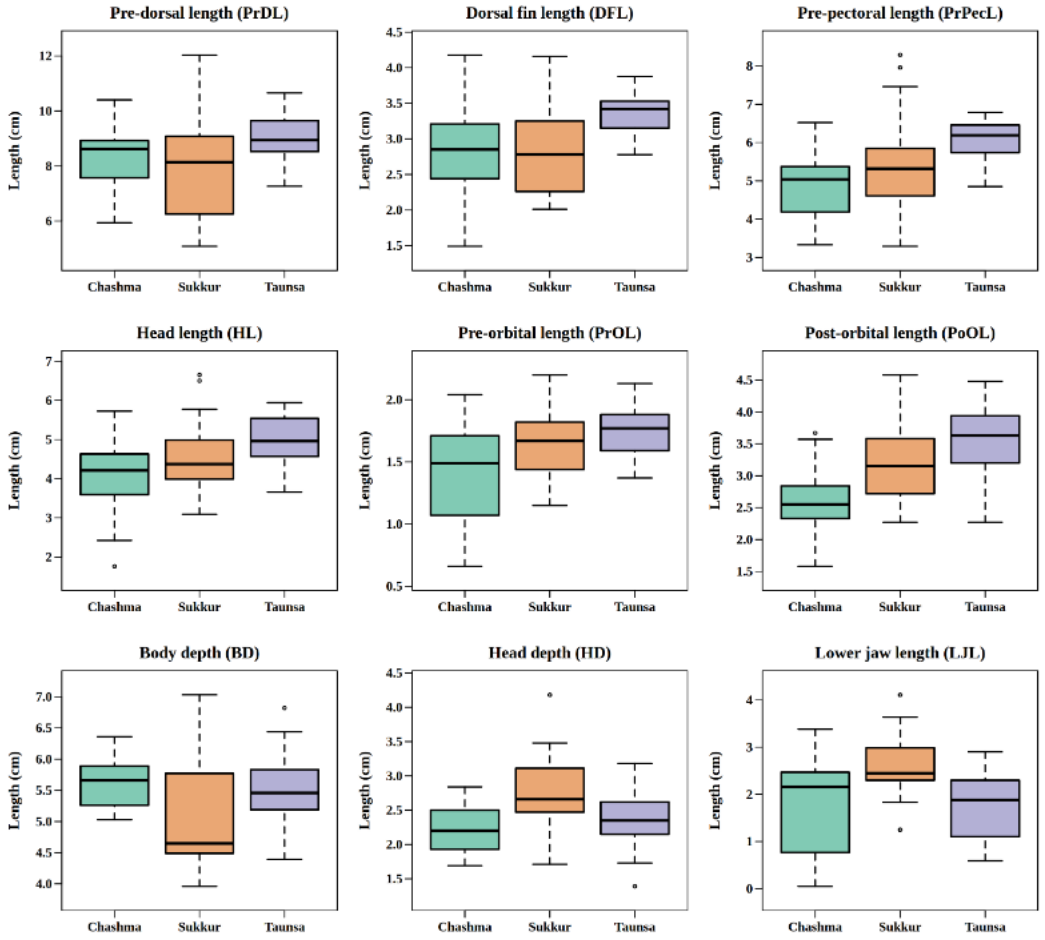


Fig.3. Box plots of nine representative morphometric characters that differed significantly among the three sites (Chashma, Sukkur and Taunsa Barrages; the full set of 13 significant characters is given in Table 2). Boxes show the median and interquartile range; whiskers extend to 1.5× the interquartile range and points are outliers.

and Taunsa Barrages, most characters grew isometrically (28 at Sukkur and 30 at Taunsa), whereas Chashma Barrage showed more frequent departures from isometry (15 positively and 11 negatively allometric characters). The length-weight relationship was negatively allometric at Chashma (b= 1.70) and Sukkur (b= 2.41) barrages and isometric at Taunsa Barrage (b= 2.08; 95% confidence interval included 3), indicating that body weight increased more slowly than expected from length at the first two sites (Fig. 4).

DISCUSSION

Morphometrics remain an extensively applied and economical technique for establishing the stock structure of commercially exploited fish based on phenotype, splitting a nominal stock into stocks that may differ in growth, condition, and productivity without regard to genetic distinctness (Rawat et al. 2017). Because body shape reflects both a fish's genotype and the environmental conditions it experiences during development, comparing body shapes between sites is a relatively easy way to detect stock structuring (Rawat et al. 2017; Kumar et al. 2023). In this study, 34 morphological variables recorded in 75 *W. attu* collected from the Chashma, Sukkur, and Taunsa Barrages of the Indus River showed highly significant differences in body shape, with 13 of 34 variables differing between sites after false discovery rate corrections. Discriminant analysis with leave-one-out cross-validation yielded an assignment accuracy of 84%, suggesting that the fish populations at the three barrages constitute phenotypically distinct stocks.

A salient feature of these findings is that the divergence occurred in shape, not size. The total, fork,

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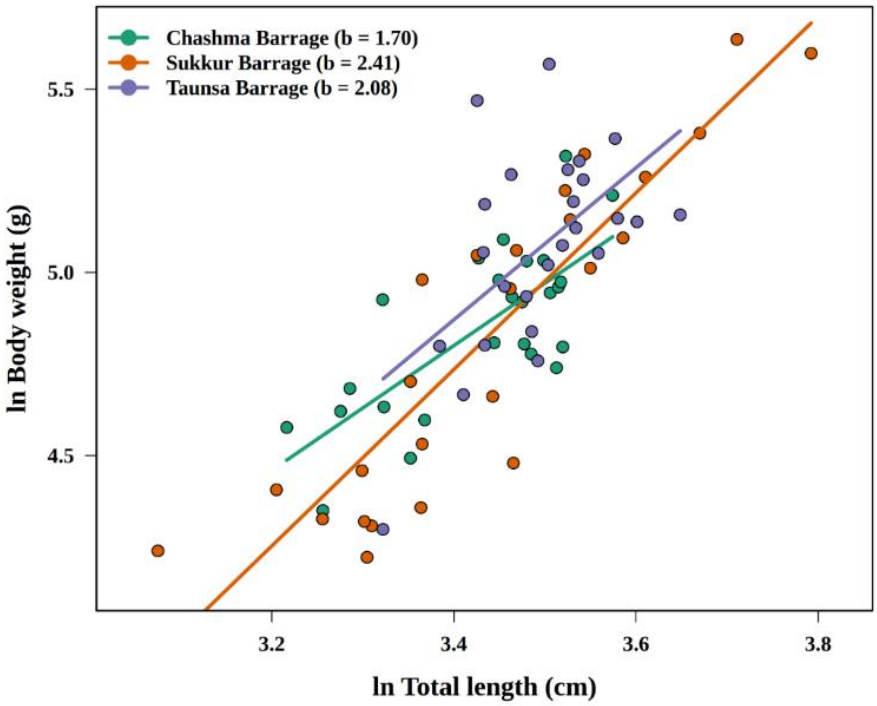


Fig.4. Length–weight relationship of *Wallago attu* at the three sites, shown as natural-log body weight against natural-log total length with site-specific fitted regression lines; allometric coefficients (*b*) are given in the legend.

and standard lengths of the fish did not vary between the three locations in any significant way, hence confirming the fact that the fish collected at the three sites had similar body lengths and that the variance seen was due to differences in body shapes after taking into consideration body sizes (Reist 1985). The variables involved included those of the head region – post-orbital length, head depth, head length, and pre-orbital length – as well as those of some fins and anterior body lengths. The trend above conforms to the findings by Kumar et al. (2023) that head-related traits (head length, eye diameter, and inter-orbital length) have high discriminative ability for *W. attu* among the five Indian rivers and, in general, the head, due to its functional roles in feeding, respiration, and sensory perception, has been identified as one of the most sensitive areas in the teleost body to environmental pressures (Klingenberg 2022). The fact that only shape varied significantly while size was controlled implies that the differences noted are not incidental but ecologically driven.

Out of the three populations, the *W. attu* from Chashma Barrage turned out to be the most morphologically differentiated in terms of having maximum multivariate divergence and near-perfect classification via the discriminant analysis while the Sukkur and Taunsa populations seemed to be more similar to each other. The Chashma fish had a shorter, shallower head and a deeper body. This makes the combination informative, given the proven ecomorphological link between body shape and hydrological regime in fishes. There has been extensive research conducted which shows that fish living in still or impounded water bodies generally have a deeper body shape with a relatively small head shape suited for maneuvering and burst swimming, while fish living in flowing water bodies have a streamlined body structure which decreases drag in sustained swimming (Langerhans 2008; Langerhans & Reznick 2010; Franssen 2011; Haas et al. 2010; Kelley et al. 2017). The Chashma Barrage impounds a larger, relatively still water body, which is an internationally important wetland with different limnological features (Kalsoom et al. 2021). Thus, Chashma Barrage represents a lentic environment compared with the other two sites, i.e., Sukkur and Taunsa Barrages, which represent a more run-of-river environment.

Table 3. Allometric growth parameters of morphometric characters of *Wallago attu* at the three sites, obtained from log–log regression on total length. b = allometric coefficient; R^2= coefficient of determination; Type= growth relative to isometry (I= isometric; A(+)= positive allometry; A(−)= negative allometry; reference *b*= 1 for lengths and *b*= 3 for body weight).

Character	F	df	*P*	*P* (FDR)	η²	Sig.	Pairwise differences (Tukey, *P*<0.05)
TL	1.98	2.72	0.146	0.186	0.052	ns	none
FL	2.32	2.72	0.105	0.163	0.061	ns	none
SL	2.82	2.72	0.066	0.132	0.073	ns	none
PrDL	5.19	2.72	0.008	0.027	0.126	*	Taunsa-Sukkur
DFL	8.44	2.72	<0.001	0.002	0.190	**	Taunsa-Chashma; Taunsa-Sukkur
PrPecL	9.10	2.72	<0.001	0.001	0.202	**	Taunsa-Chashma
PecFL	4.53	2.72	0.014	0.037	0.112	*	Taunsa-Sukkur
PrPL	2.67	2.72	0.076	0.136	0.069	ns	none
PFL	9.38	2.72	<0.001	0.001	0.207	**	Sukkur-Chashma; Taunsa-Chashma
PrAL	3.81	2.72	0.027	0.065	0.096	ns	Taunsa-Chashma
AFL	1.46	2.72	0.238	0.279	0.039	ns	none
PrOL	9.60	2.72	<0.001	0.001	0.211	**	Sukkur-Chashma; Taunsa-Chashma
ED	0.01	2.72	0.994	0.994	0.000	ns	none
HL	9.51	2.72	<0.001	0.001	0.209	**	Sukkur-Chashma; Taunsa-Chashma
PoOL	16.42	2.72	<0.001	<0.001	0.313	***	Sukkur-Chashma; Taunsa-Chashma
BD	4.63	2.72	0.013	0.036	0.114	*	Sukkur-Chashma
CFL	0.75	2.72	0.476	0.506	0.020	ns	none
BW	3.62	2.72	0.032	0.072	0.091	ns	Taunsa-Chashma
UJL	1.97	2.72	0.147	0.186	0.052	ns	none
LJL	9.22	2.72	<0.001	0.001	0.204	**	Sukkur-Chashma; Taunsa-Sukkur
CPL	0.39	2.72	0.677	0.698	0.011	ns	none
CPD	1.02	2.72	0.366	0.413	0.028	ns	none
CH	1.59	2.72	0.211	0.256	0.042	ns	none
HD	12.29	2.72	<0.001	<0.001	0.254	***	Sukkur-Chashma; Taunsa-Sukkur
PeAD	5.32	2.72	0.007	0.026	0.129	*	Sukkur-Chashma; Taunsa-Sukkur
PcAD	2.48	2.72	0.091	0.155	0.064	ns	none
PcPeD	2.75	2.72	0.071	0.134	0.071	ns	none
ACD	0.99	2.72	0.376	0.413	0.027	ns	none
ADD	2.36	2.72	0.102	0.163	0.061	ns	none
PcDD	4.95	2.72	0.010	0.030	0.121	*	Sukkur-Chashma
PcCD	1.98	2.72	0.145	0.186	0.052	ns	none
PeDD	2.13	2.72	0.127	0.186	0.056	ns	none
PeCD	2.00	2.72	0.142	0.186	0.053	ns	none
CDD	3.49	2.72	0.036	0.076	0.088	ns	Sukkur-Chashma

The morphological similarity between the Sukkur and Taunsa fish populations, despite the several-hundred-kilometer distance separating them along the river, can also be explained environmentally, since both have similar flowing-water habitats. The general trend is that the three habitats exist along a downstream gradient of the Indus, from 196 m above sea level at Chashma to 157m at Taunsa to 67m at Sukkur, where temperature, current speed, turbidity, substrate, and productivity vary. Environmental diversity drives intraspecific morphological variability among fishes, which adjust their body shape through phenotypic plasticity in response to environmental conditions (Kelley et al. 2017;

Mouludi-Saleh et al. 2018; Malik et al. 2020; Zamani-Faradonbe et al. 2020). Habitat-associated morphometric diversity has also been noted for a number of South Asian and other fishes in flowing water, such as cyprinid fishes from barrages of Pakistan (Habib et al. 2020) and farmed *Oreochromis niloticus* fish living under diverse farm conditions (Kwikiriza et al. 2023), suggesting a strong environmental impact on fish morphology.

Morphology alone cannot determine whether the separation found in this study reflects phenotypic plasticity, hereditary differentiation, or both. Molecular evidence for *W. attu* in the area appears inconclusive, as while there is a relatively high level of genetic structure among Pakistani rivers (F_ST= 0.40-0.61; Sherzada et al. 2024) using mitochondrial markers, there is only low genetic structuring among Punjab populations (mean F_ST≈ 0.03; Basharat et al. 2016) using microsatellites. The difference between the two studies is surprising, but seems to indicate that while there is indeed some sub-structuring, much of the morphological variation found among barrage populations is likely due to plasticity. However, the Indus has become highly fragmented due to multiple barrages, and *W. attu* is a potamodromous fish whose movements may be hindered by such barriers. Because in-stream barriers limit gene exchange between populations and can facilitate population differentiation in river fishes (Grill et al. 2019), further fragmentation will likely increase the phenotypic differences observed here genetically.

Allometric growth analysis offered another perspective on differences between sites. When log-transformed data were considered, most traits at Sukkur and Taunsa Barrages grew isometrically with total length, while the Chashma population showed a higher frequency of departures from isometry, corresponding to the particularity seen in the multivariate analysis. The length–weight allometry had a negative value ($b< 3$) in all three populations, showing that the fish became thinner during growth, and the condition factor was less than unity. The deviation of the length-weight exponent from the isometric exponent value of three is well known to occur because of variations in the availability of food, temperature, water quality, and the reproductive state (Bagenal & Tesch 1978; Le Cren 1951; Wootton 1990), and therefore the site-to-site variation in growth forms is plausible in light of the environmental variability at the three barrages. However, spatial variability in the length-weight and condition of *W. attu* has been reported across Indian rivers (Kumar et al. 2023). Despite the small intra-site variation in total length in the current sample, the estimated exponents are inaccurate, and coefficients for characters weakly correlated with length should be interpreted with similar caution.

These findings have important applications in managing a species considered of conservation concern due to over-exploitation and habitat degradation (Ng et al. 2020; Imran et al. 2025; Shabir et al. 2025). Based on observations of morphologically identifiable *W. attu* stocks across the three barrages, with the Chashma population particularly distinct, the Indus population cannot be treated as a single entity. Stock-specific analysis and site-specific regulation will help maintain the species' phenotypic and likely genetic diversity, and the morphometric information provided here can serve as a benchmark for future changes (Rawat et al. 2017; Sherzada et al. 2024).

However, several constraints limit these findings and highlight directions for future research. Environmental parameters such as temperature, flow velocity, and water quality have not been considered simultaneously. As a result, while the connection between morphology and habitat aligns with theory, it still involves some inference. Because the study includes only one site per habitat category, it lacks replication to identify which environmental factor drives divergence. In addition, because the study lacks genetic markers, it remains unclear whether morphology alone can distinguish plastic from genetically based variation. The current study focuses only on linear inter-landmark distance, and future studies on this ecologically and economically important catfish should use landmark-based morphometrics.

CONCLUSION

This research provides the first quantitative benchmarking of morphometric traits in *W. attu* populations from the three largest barrages of the Indus River in Pakistan and shows that, although the studied populations are generally similar in body size, they include morphologically distinct phenotypic types. Morphological differentiation was observed mainly in the head region and fin proportions, not in body size; the Chashma Barrage population is the most morphologically distinct compared with the other two populations. This finding may be attributed to the fact that fish from the Chashma Barrage live in a lacustrine environment, compared with a lotic environment at the Sukkur and Taunsa Barrages. Allometry supported these conclusions, showing more deviations from isometry in the Chashma Barrage population than in the other two populations. As the genetic distinctness of the studied barrages could not be established based on the morphological parameters, it should be investigated in future molecular studies. However, the distinctiveness of the studied phenotypes should not allow treating the Indus *W. attu* population as a single homogenous one. Given this species' Vulnerable conservation status and its ecological and economic importance, the morphometric and allometric values presented above provide a useful benchmark against which future population changes can be measured.

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مقاله کامل

آشکارسازی ساختار ریختی جمعیتی گونه *Wallago attu* در سه بند انحرافی رودخانه سند پاکستان براساس واگرایی ریختی و رشد آلومتریک

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چکیده: گونه *Wallago attu* (Bloch & Schneider, 1801) از گربه‌ماهیان خانواده Siluridae با ارزش اقتصادی بالا، به‌طور گسترده در اکوسیستم‌های رودخانه‌ای جنوب آسیا صید می‌شود. بااین‌حال، اطلاعات مربوط به ساختار ذخایر جمعیتی این گونه در جمعیت رودخانه سند در پاکستان همچنان محدود است. در پژوهش حاضر، تفاوت‌های ریخت‌شناختی میان سه جمعیت جغرافیایی متمایز از گونه *W. attu* بررسی شد که از بندهای انحرافی چشمه، سوکور و تونسا، واقع در ارتفاعات متفاوت در اکوسیستم رودخانه سند، نمونه‌برداری شده بودند. در مجموع، ۳۴ صفت ریخت‌سنجی در ۷۵ نمونه (۲۵ نمونه از هر منطقه) با استفاده از روش نقطه لندمارک (Landmark Method) اندازه‌گیری شد. سپس، تحلیل‌های چندمتغیره، تک‌متغیره و آلومتریک انجام گرفت. نتایج تحلیل واریانس چندمتغیره (MANOVA) نشان داد که شکل بدن در میان سه جمعیت *W. attu* تفاوت معنی‌داری دارد (Pillai's trace = 1.49, $F_{(26, 122)}$= 13.80, P<0.001). از میان ۳۴ صفت بررسی‌شده، ۱۳ صفت پس از اعمال اصلاح نرخ کشف کاذب (False Discovery Rate; FDR) تفاوت معنی‌داری نشان دادند؛ درحالی‌که طول کل، طول چنگالی و طول استاندارد در میان سه جمعیت تفاوت معنی‌داری نداشتند. این یافته نشان می‌دهد که تفاوت معنی‌داری از نظر اندازه بدن میان سه جمعیت وجود نداشته است. بااین‌حال، نسبت‌های بدنی، به‌ویژه ویژگی‌های ناحیه سر و باله‌ها، تفاوت‌های معنی‌داری را نشان دادند؛ از جمله طول پس‌چشمی ($\eta^2 = 0.31$) و ارتفاع سر ($\eta^2 = 0.25$). تحلیل مؤلفه‌های اصلی (PCA) نشان داد که جمعیت‌ها در امتداد محور نخست، که ۵۳/۲ درصد از تغییرات را تبیین می‌کرد، از نظر اندازه همپوشانی داشتند؛ اما در امتداد محورهای مرتبط با شکل بدن، جدایی نسبی مشاهده شد و گروه چشمه متمایزترین خوشه را تشکیل داد. تحلیل تشخیصی با اعتبارسنجی متقاطع نیز توانست ۸۴ درصد از افراد را به‌درستی به محل منشأ آنها نسبت دهد. الگوی رشد آلومتریک در نمونه‌های سدهای سوکور و تونسا ایزومتریک بود. در مقابل، رشد غیرایزومتریک در میان ماهیان چشمه غالبیت بیشتری داشت. همچنین، رابطه طول-وزن در نمونه‌های چشمه و سوکور از آلومتری منفی پیروی کرد، درحالی‌که این رابطه در نمونه‌های سد تونسا ایزومتریک بود. نتایج این پژوهش نشان می‌دهد که نمونه‌های جمع‌آوری‌شده از سه بند انحرافی، بیانگر ذخایر فنوتیپی متمایز از نظر ویژگی‌های ریخت‌شناختی هستند. این تمایزها به‌احتمال زیاد تحت تأثیر تفاوت‌های زیستگاهی میان محیط‌های آب ساکن (لنتیک) و آب جاری (لوتیک) در رودخانه سند قرار دارند.

کلمات‌کلیدی: *Wallago attu*، ریخت‌سنجی، رشد آلومتریک، ذخیره فنوتیپی، رودخانه سند، واگرایی جمعیت‌ها