Zoology and Ecology, 2023, Volume 33, Number 1
Online ISSN: 2165-8013
https://doi.org/10.35513/21658005.2023.1.8

MORPHOMETRIC DIFFERENTIATION OF *LABEO CATLA* (HAMILTON 1822) (CYPRINIDAE) IN RIVERS: POSSIBLE ADAPTATION TO HYDROLOGY

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Suresh V.R., Naskar M., Brahmane M.P., Prusty A.K., Panda D., Behera B.K., Sajina A.M., Sahu S.K., Meena D.K., Lal K.K. 2023. Morphometric differentiation of *Labeo catla* (Hamilton 1822) (Cyprinidae) in rivers: Possible adaptation to hydrology. *Zoology and Ecology* 33(1), 63–76. https://doi.org/10.35513/21658005.2023.1.8

Article history
Received: 5 December 2022; accepted 08 May 2023

Keywords:
Morphometry; Catla; Ganga; Narmada; truss network; multivariate analysis; phenotypic plasticity

Abstract. Morphological differentiation in the Indian major carp, *Labeo catla,* in the Ganga and Narmada rivers was studied using image-based morphometric and multivariate analytical techniques. Twenty-three truss-network-based distances connecting 11 anatomical landmarks on the fish were measured from the digital images of the specimens collected from seven stations, four of which were set up along the river Ganga, and the other three stations along the river Narmada. For analysis, five stations were considered, as the samples from the three stations on the River Narmada were pooled and treated as a composite sample (Narmada). The multivariate analysis of variance showed evidence for significant morphometric differences between samples collected from the Ganga and those from the Narmada rivers. The subsequent Linear Discriminant Analysis explained 86% of the variability between the stations by two discriminant functions. This fact suggested the existence of three morphometrically different populations of the species along the Ganga. These populations were predominantly distributed in the middle stretch of the river (Ganga_Middle), the Bhagirathi-Hooghly stretch, and the Padma stretch, which are isolated by a barrage that does not allow free bidirectional movement of fish. The important discriminating morphometric characteristics were traits from the head and caudal region as well as the body depth of fish. The relatively narrower angles of snout profiles and lower body depths of the studied fish in populations from the Padma and Bhagirathi-Hooghly stretches of the River Ganga led to more pointed snouts and slenderer bodies. Morphological differentiation can be used as an environmental predictor that, in turn, would be of use in developing effective management strategies for the fish species of stock management concern.

INTRODUCTION

Multiple studies that have been carried out to date report a morphometric variation within the riverine fish species, which consist of geographically isolated populations due to natural or manmade barriers (Meldgaard et al. 2003; AnvariFar et al. 2011; Dwivedi et al. 2019; Dwivedi 2021). Analysis of intraspecific morphometric variation is considered to be an important tool for assessing the species population structure (Cadrin and Friedland 1999; Turan 2004), mediated by environmental or genetic attributes (Domenici 2003; Ndiwa et al. 2016). Morphology of stream fishes, which varies with hydrological conditions (Pough 1989), influences their swimming performance (Ojanguren and Braña 2003). Image-based morphometric analysis has been effectively used to investigate morphometric differentiation in fish. Some such examples from different locations of freshwater and marine areas are *Trachurus trachurus* (Murta et al. 2008), *Megalaspis cordyla* (Sajina et al. 2011a), *Rastrelliger kanagurta* (Sajina et al. 2011b), *Decapterus russelli* (Sen et al. 2011), *Schizothorax richardsonii* (Farook et al. 2013), *Labeo catla* (Sarkar et al. 2014), *Nemipterus japonicus* (Sreekanth et al. 2015), *Cirrhinus mrigala* (Dwivedi et al. 2019; Dwivedi 2021), *Garra rufa* (Saemi-Komsari 2021), and *Scorpaena* spp. (Yedier and Bostanci 2021).

Several studies have focused on the effects of geographical isolation and environmental attributes on the morphological differentiation in stream fishes (Haas et al. 2010; Franssen 2011; Foster et al. 2015; Ndiwa et al. 2016; Radkhah et al. 2017; Shukla and Bhat 2017) and also on changes in fish populations induced by physical barriers to longitudinal connectivity and or habitat/hydrological alterations, including current velocity and discharge (Marcil et al. 2006; Langerhans 2008; Haas et al. 2010; Hossain et al. 2010; Paknejad et al. 2014; Vatandoust et al. 2015; Foster et al. 2015; Radkhah et al. 2017; Shukla and Bhat 2017; Dwivedi 2021). Several previous studies have examined differences in specific morphometric traits in fish populations along the river stretches with differing hydrological gradients (Hendry et al. 2006; Haas et al. 2010; Schaefer et al. 2011; Jacquemin et al. 2013; Shukla and Bhat 2017). These studies could also provide insights into the impacts of isolation and hydrology on fish populations and the evolutionary adaptive significance of such differentiation.

The Ganga and Narmada rivers are among the large rivers in India that are geographically isolated in different basins. The River Ganga, originating from the Western Himalayas and flowing towards the northeastern coast of India, traverses 2525 km before draining into the Bay of Bengal (Jain et al. 2007). The River Narmada, originating from the Maikala ranges of the Amarkantak hills in Madhya Pradesh, flows towards the northwestern coast of India, covering 1312 km before draining into the Arabian Sea (Jain et al. 2007). These rivers support the natural populations of the Indian major carp catla, *Labeo catla* (Hamilton 1822) (Jhingran 1968). The species has high economic importance in the region (Vass et al. 2010), however, their populations are declining fast in these rivers (Payne et al. 2004). Several dams and barrages that act as physical barriers have been built across these rivers. The species being potamodromous and benthopelagic (Riede 2000), dams and barrages obstruct their free bidirectional movement (Dwivedi 2021) and lead to changes in its fisheries as well as in its distribution, morphometric and biological traits (Rao 2001; Dwivedi 2021).

The occurrence of morphometric variations among *L. catla* populations in the River Ganga and in its two tributaries within the same basin (rivers, Betwa and Ken) have already been reported (Sarkar et al. 2014), and these differences were attributed to physical and ecological parameters. In the light of the above, we hypothesized that hydrological differences and isolation may lead to evolutionary morphological adaptations in *L. catla*, which is large-bodied, benthopelagic, potamodromous (Riede 2004), and relatively non-habitat-selective. This in turn would help morphology-based delineation of stocks in the rivers that are of use for stock-specific management interventions as the fishery of the species in the rivers is declining. Information on the morphometric changes in populations of the species due to hydrology- and isolation-related differences would expand knowledge on the impact of altered environmental flows on fish species and would help future studies into the phenotypic predictors of adaptation to environmental changes (Matt et al. 2017).

In the present study, we used multivariate analysis of the selected, size-free landmark-based morphometric traits of *L. catla,* collected from its distribution ranges in the Ganga and Narmada rivers, to assess morphometric differentiation and link it to the possible evolutionary adaptations to hydrology.

METHODS

Sample collection

Samples of *L. catla* were collected from seven stations (Figure 1), four of which were set up along the River Ganga (Allahabad, Patna, Beniagram, and Nabadwip) and three along the river Narmada (Bharuch, Sinor, and Surpan). The Allahabad and Patna stations were situated in the middle stretch of the river Ganga, where the bidirectional movement of the species between these stations was possible. The Beniagram station (5 km downstream of the Farakka barrage) was situated in the main course of the River Ganga flowing from India into Bangladesh as the river Padma before merging with the Bay of Bengal. The Nabadwip station was set up in the Bhagirathi-Hooghly stretch of the river, passing through India, before merging with the Bay of Bengal (Figure 1). The bidirectional movement of fish between Beniagram and Nabadwip, and these stations with Allahabad and Patna is restricted. Until 1975, the lower stretch of the Ganga was unregulated, but the Farakka barrage, commissioned across the River Ganga in West Bengal in 1975 (Animesh and Carlo 2014), restricted the bidirectional movement of fish along the main river channel. After the Farakka barrage commissioning, water from the main limb of the Ganga is diverted through a lock-gate into a feeder canal connecting the Bhagirathi-Hooghly distributary of the Ganga passing through India before merging into the Bay of Bengal. The Bhagirathi-Hooghly distributary is not connected with the main limb of the Ganga downstream of the Farakka barrage. Hence, the free mixing of the breeding populations of the species among the three stretches of the river is restricted. The hydrology in terms of current velocity and discharge also differs among these stretches.

On the River Narmada, study stations were set up at Bharuch, Sinor and Surpan (Figure 1). Although they are connected, they are naturally isolated from the River Ganga as the Narmada belongs to a different basin with differing hydrology. The number of samples collected from each station on the river Narmada was low. Therefore, the samples collected from three stations were pooled and treated as a composite sample representing the river. Hence, only five data sets were considered in the analysis.

Fish samples were collected from boat-fishing catches in the open river using gill nets of various mesh sizes and cast nets and traps in shallower marginal areas, to ensure that the origin of the samples is linked to the respective river stretch. Specimens representing all available size groups in fishermen's catches (small, medium, large and intermediaries) were sampled from a 10 km stretch of each of the stations. All stations in both rivers were sampled within the same quarter of the year to ensure the uniformity of the sampling period. Due to the absence of external sexual dimorphism and difficulty in sexing all the specimens, male and female specimens were pooled for the study. Gravid specimens with swollen abdomens were eliminated from the samples because of the possible difference in the general shape. During monsoon, when the species spawned, samples were not collected. Sample sizes from upstream locations of both rivers were not adequate and, hence, could not be included in the study.

Image digitization

Digital images of the specimens were captured in the field after cleaning each specimen with a towel and placing it on a 10 mm cell graph paper spread on a flat surface. The fish was laid on its right side with the head facing the left side. The graph paper was used for calibrating the coordinates of digital images while measuring the truss distance. The fins of the specimens were stretched in natural positions to make their origin and insertion visible. Digital images of each specimen were captured from directly above the specimens, keeping them in the centre of the image using a DSLR camera (Canon EOS 1500D) mounted on a tripod to make sure that the plane of the image sensor was parallel to the surface on which the fish was positioned.

Truss distance measurement

The truss distance measurement protocol used was based on 11 morphological landmarks, marked on the

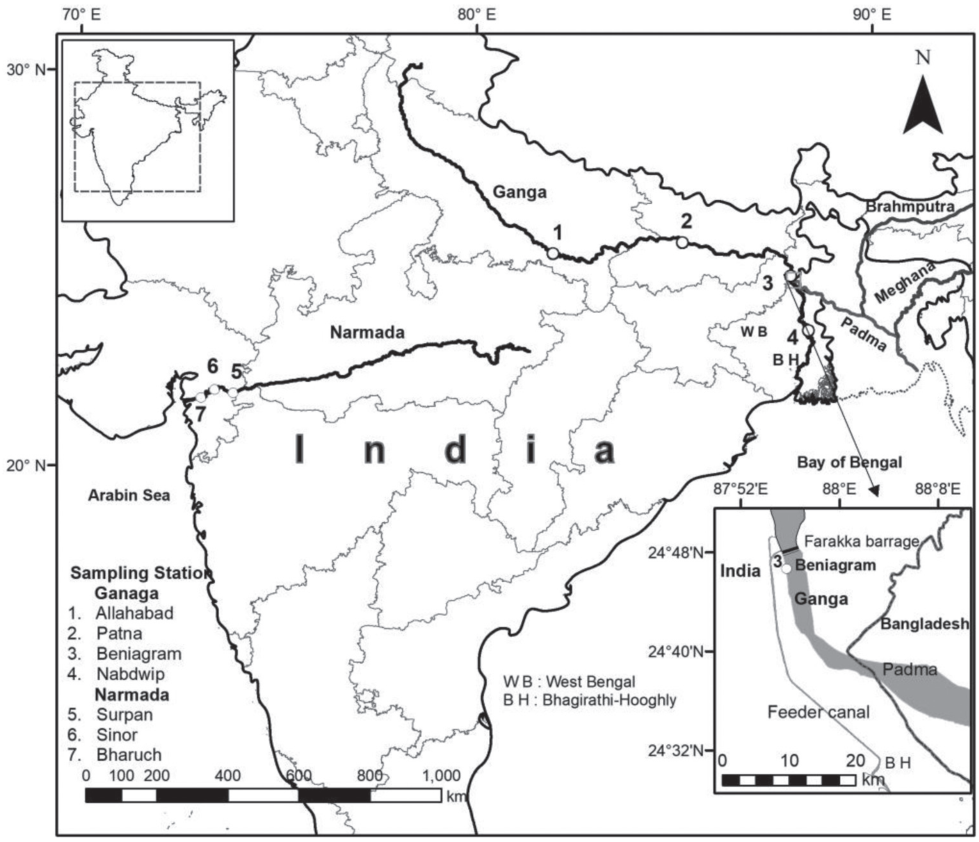

Figure 1. Location of sample collection stations along the Ganga and Narmada rivers.

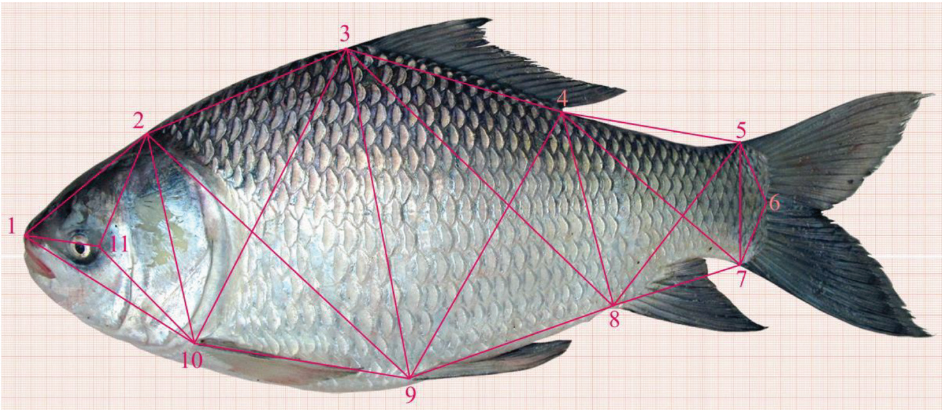

Figure 2. Image of *L. catla,* showing 11 morphological landmarks and lines of truss network selected for measurement of the distance between the landmarks. Landmark 1 is the anterior tip of the snout on the upper jaw, 2 is the posterior edge of the supraoccipital bone, 3 is the anterior origin of the dorsal fin, 4 is the insertion point of the last dorsal fin ray of the dorsal fin, 5 is the dorsal origin of the caudal fin, 6 is the intersection point of the lateral line on the caudal fin, 7 is the ventral point of origin of the caudal fin, 8 is the origin of the anal fin, 9 is the anterior origin of the pelvic fin, 10 is the origin of the first pectoral fin spine, and 11 is the posterior edge of the eye.

digital images of fish (Figure 2). A truss network of these landmarks was then built by interconnecting 11 anatomical landmarks, resulting in 23 truss distances (TD). The distances between the 11 landmarks along the 23 truss network coordinates were measured digitally, in cm scale, using a sequential combination of two software platforms, tpsDig2 v2.1 (Rohlf 2006) and Paleontological Statistics (PAST) (Hammer et al. 2001). Fish images were converted into the tps format using the utility program tpsUtil, and the landmarks were marked on the tps image file using the tpsDig2 software. The distances between the landmarks were extracted from the landmark saved image files using PAST. The distance between landmarks 1 and 6 (TD1_6) was taken as the standard length (SL) of the fish (Figure 2).

Elimination of size effect on the shape

In multivariate morphometric data of natural fish populations, variability arises due to individual size differences. As size is associated with individual growth, for classification purposes, the shape of the fish characterized by TD values should be size-independent. This was accomplished by eliminating allometric growth variation. First, the strength of the relationship between TD measurements and standard length (SL) was evaluated based on R^2 values between SL and each TD on the log scale. Then, the TD values were adjusted for growth variation to an overall mean of standard length (Reimchen et al. 1985; Senar et al. 1994) as follows:

$$\mathrm{TD}'_{ij} = \log(\mathrm{TD}_{ij}) - b_j\{\log(\mathrm{SL}_{ij}) - \log(\mathrm{SL}_m)\}$$

where TD'_{ij} and TD_{ij} are the adjusted and measured values, of the *j*-th TD value for individual *i,* respectively; b_j is the pooled regression coefficient of log (TD) on log (*SL*) for the *j-th* TD*;* SL_{ij} is the standard length of individual *i* for the *j*-th TD; and SL_m is the overall mean standard length.

Elimination of outliers

The adjusted TD values were then subjected to outlier elimination by applying the Mahalanobis distance measure, defined as

$$\mathrm{D}_i^2 = (\mathrm{TD}_i - \mu)'\textstyle\sum^{-1}(\mathrm{TD}_i - \mu);$$
$$\text{for } i = 1,2 \ldots n \text{ (= number of specimens).}$$

Outliers were detected by visual inspection of the plot of D_i^2 against the *i-th* specimen.

Discriminating samples

The Multivariate Analysis of Variance (MANOVA) was carried out to examine the statistical significance of morphometric differences among the samples collected from different stations. Then, Linear Discriminant Analysis (LDA) was applied to discriminate specimens from different stations, assuming the prior probability of class (here station) membership as the proportional sample size of each class (here station). The resulting bi-plot corresponding to the two most important discriminant functions was examined to determine the number of distinct classes. LDA was further reapplied with newly formed classes in which specimens of majorly overlapping classes were pooled. The accuracy of classification has been evaluated by comparing the observed and predicted classes of specimens. For more specificity, a confusion matrix between the predicted class (station) and observed class (station) was constructed. Thereafter the average error rate (AER) (or misclassification rate) and Station Specific Error Rate (SSER) were computed as follows.

$$\text{AER} = \frac{\text{Total number of misclassified specimens}}{\text{Total Number of specimens in the sample}}$$

$$\text{SSER} = \frac{\text{Number of misclassified specimens in a station}}{\text{Total number of specimens in a station}}$$

Identification of discriminating characters

After satisfactory discrimination with the desired classification accuracy, the relative importance of each character for discrimination was determined. The actual discriminatory power depends on the score of the resulting discriminating function, a linear combination of TD characters. However, the interpretation of the derived synthetic function is difficult. It is always desirable to interpret in terms of original characters. Therefore, the contribution of a character to the derived function, typically measured as the correlation between the linear discriminating function and original variables, is used to measure the relative power of discrimination of the original character. Thus, a relatively high correlation of a character, as compared to others, indicates a relatively higher discriminatory power of a character.

The significant characters that discriminate specimens were further used for the discrimination based on shape, especially that of snout. To this end, the angles of the triangle formed by the most discriminating TD were used; and the Cosine Law of Triangle was used to compute the angle using the generic equation as follows:

$$\theta_a = cos^{-1}\left(\frac{a^2+b^2-c^2}{2ab}\right); \theta_b = cos^{-1}\left(\frac{a^2+c^2-b^2}{2ac}\right);$$
$$\theta_c = cos^{-1}\left(\frac{b^2+c^2-a^2}{2bc}\right),$$

where a, b and c are sides of the triangle; and θ_a, θ_b and θ_c are angles opposite to sides a, b and c, respectively, of the triangle. Further, one-way ANOVA and post hoc 'TukeyHSD' (Tukey 1949) were applied to examine significant differences in the angle among different groups.

Hydrology

Although no data are available on the micro or macro habitat preference of the species, from our sample collection experience, the fish was caught from across the river covering near-shore and far-shore areas without any noticeable congregation at any specific locations of the river. All sampling stations had perennial flows. Hence, the hydrology data in terms of mean annual current velocity and discharge were collected from available literature and reports, though detailed data are classified due to national interests.

All the statistical analyses were performed using the necessary libraries, including 'MASS, 'ggplot2', and 'candisc', under the R Software (R Core Team 2019) environment.

RESULTS

The number of samples collected from each of the sampling stations along the Ganga and Narmada (pooled), their SL ranges, and mean SLs (Table 1) showed wide variations. The samples comprised a mix of juveniles and adults. Samples from Allahabad were mostly mid-size and those from Patna were mostly a mix of smaller and larger sizes due to the selectivity of local fishing gear used by fishers depending on the market and trade dynamics. The frequency distributions (Figure 3) of samples of different SL groups from each station were not the same; they were skewed or bimodal, indicating at least more than two size groups in catches from each station. The scatter plot of all the TD measurements against SL on a log-log scale (Supplementary Figure 1) revealed linear relationships between TD and SL and all the R^2 values were in the range of 0.80–0.95. This established an allometric growth of the TD concerning SL; thereby log transformation of TD values to eliminate the size effect was justified with a high degree of reliability. The outlier diagnostic plot (Supplementary Figure 2) showed one outlier, which was eliminated from the data set before further analysis.

Results of the MANOVA showed that the statistical test based on Pillai's trace statistics was highly significant (Pillai's trace = 1.80; Approx. F = 9.868; Df = 4,296; and $p < 0.001$). Linear Discriminant Analysis (LDA) was applied in two stages. Its first stage application generated four linear discrimination (LD) functions (LD1, LD2, LD3 and LD4); they respectively captured 61.31% (LD1), 16.82% (LD2), 13.78% (LD3) and 8.09% (LD4) of between-station variability. The two most important functions were LD1 and LD2, accounting for a reasonably high (78.13%) variability. The bi-plot of LD1 and LD2 suggested indistinguishable centroids of Allahabad and Patna, occupying an almost identical space (Figure 4). Hence, they were grouped as the Ganga_Middle; the other groups were Beniagram, Nabadwip and the Narmada, which remained the same. Thus, the first stage analysis resulted in four groups.

The second stage of LDA involved the four groups that had been identified in the first stage. It resulted in the measure overall AER of classification of 12.29%; and

Table 1. Details of samples collected (numbers and SL range) from each location.

Rivers	Stations	n	SL ranges (cm)	Mean SL (cm)
Ganga	Allahabad	56	22.24–60.28	40.72
	Patna	68	15.96–91.25	76.78
	Beniagram	73	25.39–70.12	34.40
	Nabadwip	53	19.02–74.35	31.74
Narmada	Pooled	54	25.06–37.97	31.43

SL: Standard length.

the SSER of the Ganga_Middle, Beniagram, Nabadwip and the Narmada were 8.13%, 17.81%, 12.68% and 14.70%, respectively (Table 2).

The two most important discriminant functions, LD1 (67.43%) and LD2 (18.51%), cumulatively captured 86% between-station variability, which indirectly signified the merging of overlapping groups- Allahabad and Patna; the resultant LD1 is the most important index for discriminating specimens among stations. Further, TD1_2, TD1_10, TD1_11, TD2_3, TD4_9, TD9_10, TD3_9, and TD4_5 were the most important morphometric characters for discriminating the specimens (Figure 5), setting a cut-off correlation coefficient greater than or equal to 0.5. While TD3_9 and TD4_5 represent LD2, the remaining characters represent LD1. Further, the pairwise absolute correlation between LD1 and TD1_2, TD1_10, TD1_11, TD2_3 and TD2_9 was as high as 0.70; thereby, those were representatives of LD1 and were approximately taken as the most important discriminating morphometric character. Albeit, TD3_9 and TD4_5, being representative of LD2, also have relatively higher discriminating power than others. The variability (standard deviation)

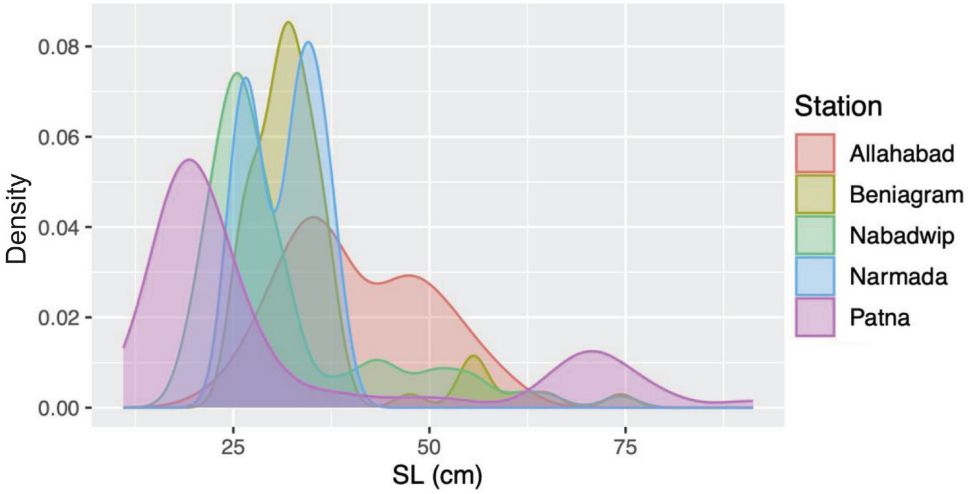

Figure 3. Station-wise standard length frequency distribution of *L. catla*.

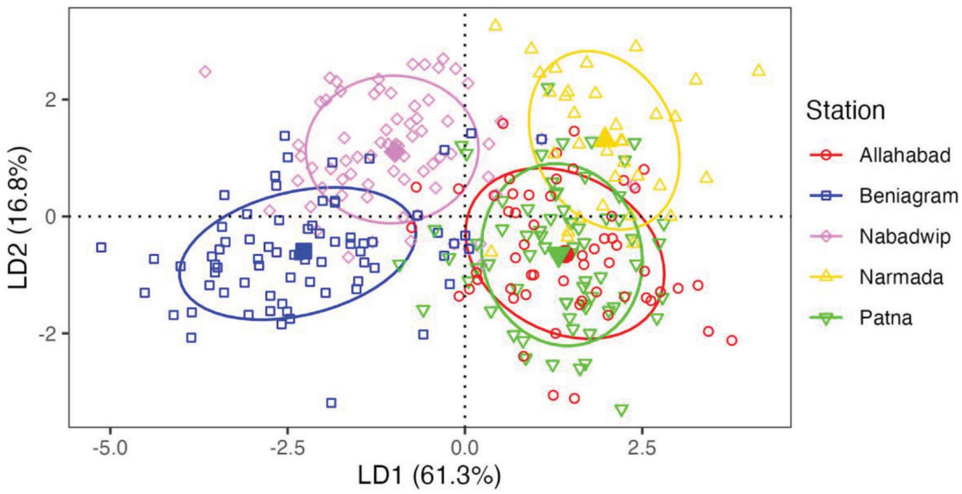

Figure 4. Bi-plot of the discriminant score of specimens. The centroids of each ellipse are indicated with filled symbols corresponding to the stations. The ellipses represent the 80% confidence region.

Table 2. Confusion matrix based on the observed and predicted class, showing the number of observations and percentage (%) classified (within parenthesis) into stations.

Stations	Ganga_Middle	Beniagram	Nabadwip	Narmada	Total
Ganga_Middle	113 (91.87)	2 (1.63)	5 (4.07)	3 (2.44)	123 (100)
Beniagram	7 (9.59)	60 (82.19)	6 (8.22)	0 (0.00)	73 (100)
Nabadwip	7 (9.86)	2 (2.82)	62 (87.32)	0 (0.00)	71 (100)
Narmada	5 (14.71)	0 (0.00)	0 (0.00)	29 (85.29)	34 (100)
Total	134 (43.85)	64 (21.26)	73 (24.25)	32 (10.63)	301 (100)

is almost similar for all the characters, but perceptible differences in the mean TD values existed among stations (Table 3); mean values of TD1_2, TD1_10 and TD1_11 were relatively higher in the lower stretch (Beniagram and Nabadwip) than in the Ganga_Middle stretch (Allahabad and Patna); on the contrary, mean values of TD2_3 and TD2_9 were relatively lower in the lower stretch than in the Ganga_Middle stretch and mean TD2_3 and TD3_9 of the Narmada were relatively high in comparison to the stations along the Ganga. The five distances (TD1_2, TD1_10, TD1_11; TD2_3 and TD2_9), highly associated with LD1, were from the head region of the samples, while TD3_9 represented the body depth and TD4_5 represented the tail region (Figure 2). For each specimen, the angle of snout profile (the angle formed between TD1_2 and TD1_10 of the triangle with sides TD1_2, TD1_10 and TD2_10) was computed. The mean angle of the snout profile for samples collected from the Narmada was the widest (64.1°); followed by that of the samples from the Middle stretch of the Ganga (62.8°), Nabadwip (60.4°) and the narrowest angle was recorded in specimens from Beniagram (58.9°) (Figure 6a). One-way ANOVA established a highly significant difference ($p \leq 0.001$) in the angle of snout profile among the groups. The pair-wise Tukey HSD test showed that the mean of the angle of the snout profile significantly differed between all the pairs of stations (Supplementary Table 1). Similarly, the body depth (TD3_9) of specimens of a similar size range (30.65–31.35 cm SL; size uncorrected), chosen as a subset of the data from different stretches of the river for comparison (sub-sample sizes (no.) for Narmada = 37, Nabadwip = 48, Beniagram = 54, and Middle_stretch = 50), also differed between the Ganga and Narmada populations significantly with deep bodied specimens in the Narmada compared to those from the Ganga (Figure 6b). In stretches of the River Ganga, the lowest body depth was found in specimens from Beniagram representing the Padma stretch of the river. We also examined the ratios between SL and body depth (TD3_9) of all the specimens collected from different stations (Table 4), which showed a higher SL/depth ratio for specimens from the Padma stretch and the lowest for Narmada samples, corroborating the results in Figure 6b.

The hydrological data (Table 4) showed a significantly faster annual mean current velocity (0.40 m s^{-1}) and a higher annual mean discharge rate (18.490 m^3 s^{-1}) in the River Ganga than in the River Narmada (0.22 m s^{-1} and 1216 m^3 s^{-1}). The parameters in different stretches of the River Ganga differed significantly too with a faster current along the Padma (1.99 m s^{-1}) and Bhagirathi-Hooghly (0.53 m s^{-1}) stretches and the highest discharge in the Padma (30000 m^3 s^{-1}) stretch. The River Narmada has the lowest current velocity (0.22 m s^{-1}) and discharge rate (1216 m^3 s^{-1}) of all the River Ganga stretches.

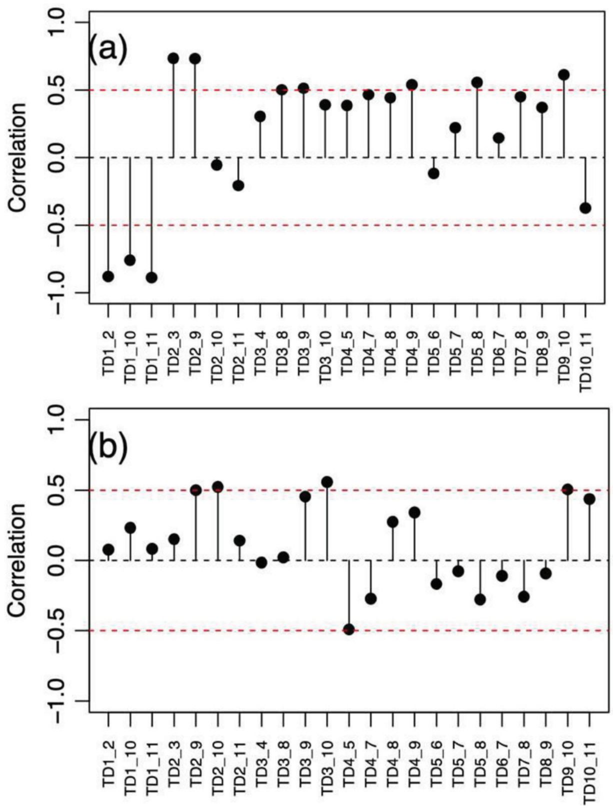

Figure 5. Correlation coefficients of morphometric characters (TD) with two most important discriminant functions, the LD1 (a) and LD2 (b). The dotted red lines denote the threshold for the most important discriminating TD.

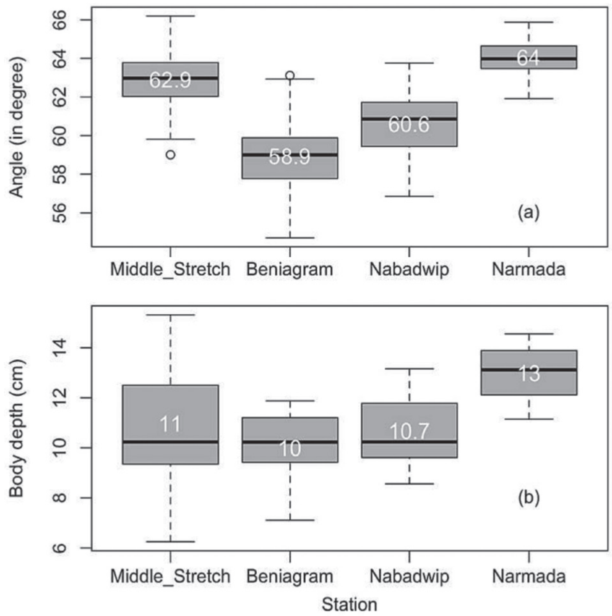

Figure 6. (a) Box plots showing variation in the angle of snout profile and (b) body depth (TD3-9) of specimens from different river stretches. The data used are not size-corrected but belong to a sub-sample ranging in size from 30.65 to 31.35 cm SL that is present across all the stations. The values within each box represent the mean and the lines represent the median.

Table 3. Comparison of mean and standard deviation SD (within parenthesis) of the linear discriminant function of the size-corrected TD for morphometric discrimination among groups.

Groups	LD1					LD2	
	TD1_2	TD1_10	TD1_11	TD2_3	TD2_9	TD3_9	TD4_5
Ganga_Middle	2.07 (0.062)	2.18 (0.062)	1.18 (0.123)	2.32 (0.049)	2.71 (0.036)	2.57 (0.057)	1.81 (0.074)
Beniagram	2.25 (0.075)	2.29 (0.052)	1.49 (0.122)	2.22 (0.061)	2.64 (0.037)	2.4t9 (0.050)	1.78 (0.090)
Nabadwip	2.19 (0.073)	2.27 (0.062)	1.39 (0.102)	2.27 (0.055)	2.70 (0.032)	2.57 (0.046)	1.69 (0.114)
Narmada	2.07 (0.051)	2.22 (0.058)	1.17 (0.125)	2.35 (0.065)	2.75 (0.029)	2.57 (0.039)	1.80 (0.089)

LD1: the first linear discriminant function; LD2: the second linear discriminant function; and TD: Truss distance.

Table 4. Station-wise mean angle of the snout profile, body depth and the SL/Depth ratios in relation to the mean velocity and discharge of the river stretches.

River/ Stretch	Snout profile (angle °)	Body depth (cm)	SL/depth (Ratio)	Mean velocity ($m\ s^{-1}$)*	Mean discharge ($m^3\ s^{-1}$)*
Ganga main	62.8^a	11.67^a	2.68^a	0.40^a	18.490^a
**B–H stretch	60.4^b	10.67^b	2.66^a	0.53^a	12.473^b
Padma stretch	58.9^c	9.99^c	2.82^b	1.99^b	30.000^c
Narmada	64.1^d	12.99^d	2.62^a	0.22^c	1.216^d

*Source: Gupta and Chakrapani (2007), Neill et al. (2013), Raghunath and Padmini (2016), Mahmud et al. (2017). **Bhagirathi-Hooghly. Values in each column with different superscripts differ significantly.

DISCUSSION

Differences in environmental factors, altitude gradients, geographical location, hydrological conditions, habitat diversity, etc., are known to influence the morphological differentiation among fish populations (Hendry et al. 2002; Herczeg et al. 2010; Foster et al. 2015; Ndiwa et al. 2016; Jearranaiprepame 2017; Yedier and Bostanci 2021). In the present study, the results of MANOVA provided strong evidence for a morphometric difference between specimens from the Ganga and those from the Narmada rivers and among specimens from different stretches of the River Ganga, suggesting the existence of four distinct morphotypes distributed along (i) the Allahabad-Patna stretch of the Ganga (Ganga_Middle), (ii) the Bhagirathi-Hooghly stretch represented by the Nabadwip station, (iii) the Padma stretch represented by the Beniagram station and (iv) the Narmada River. This has been subsequently substantiated by a relatively lower in-sample misclassification rate of 12.29%. The Ganga and Narmada rivers are naturally isolated in different basins and fish populations cannot mix. Within the Ganga, the bidirectional movement of fish along the Allahabad and Patna stretches is possible as the species is potamodromous, the river stretch is in a continuum with free flows all along this stretch. The Farakka barrage, built across the river, has been obstructing the free mixing of the breeding populations of the species from the middle stretch of the river with those from the Bhagirathi-Hooghly stretch and the Padma stretch since 1975. However, during the years of heavy rainfall and flooding, the water level on both sides of the barrage occasionally levels up and some individuals may cross over the river through the gaps of the shutters. The Narmada and the three stretches within the Ganga River also differ in hydrology in terms of current velocity and discharge rates. In the long run, the geographic isolation and environment/habitat differences that restrict the inter-mixing of breeding populations and the resultant gene flow, can manifest in morphometric differences (Wainwright and Reilly 1994; Eklöv and Svanbäck 2006; Yamamoto et al. 2006). Man-made barrages impact connectivity, which may isolate riverine fish populations (Reid et al. 2008), resulting in changes in population structure and morphological differences in the long run (Esguícero and Arcifa 2010). Meldgaard et al. (2003) reported that weirs built across rivers constrained the bidirectional migration of *Thymallus thymallus,* resulting in morphological variation in their population. Similar impacts were reported in *Capotes capoeta gracilis* (AnvariFar et al. 2011) and *Cirrhinus mrigala* (Dwivedi 2021). The species, *L. catla,* being potamodromous, has ample opportunities for the mixing of populations, and the gene flow within the Middle-Stretch of the Ganga, which is free flowing in a continuum and the environment is by and large similar (Vass et al. 2010), results in a high degree of morphometric similarity between the Allahabad and Patna specimens. However, the natural isolation of populations in the Ganga and Narmada rivers and decades of restricted gene flow of the populations among the three stretches within the River Ganga coupled with the consequent difference in hydrology may have resulted in morphometric differentiation among the populations.

The most significant truss distances that differentiated *L. catla* were from the head and anterior part (TD1_2, TD1_10, TD1_11, TD2_3, and TD2_9), the caudal region (TD4_5), as well as the body depth (TD3_9). The variations in the shape of the head, body depth, and tail region, collectively contributed to the morphometric difference among the populations. The shape of the head, body depth and tail region of fish are important for locomotion (Haas et al. 2010), which in turn is influenced by local hydrology (Haas 2015; Radkhah et al. 2017).

Labeo catla is a benthopelagic, potamodromous, surface and mid-water feeder; its spawners migrate towards the littoral zones of flood plains during the monsoon season; spawn and fingerlings mostly congregate closer to the shore (Jhingran 1968). The species is fished from across the open benthopelagic realm of the river. Hence, we considered the mean annual flow and velocity as the main hydrology parameters. The angle formed by TD1_2 and TD1_10 that shapes the snout, which is highly associated with LD1, had the highest discriminatory power. Hence, the angle formed between TD1_2 and TD1_10 was considered as an additional factor for discriminating the population of the species. The mean angle between TD1_2 and TD1_10 is the widest for samples from the Narmada, followed by the Ganga_Middle, Bhagirathi-Hooghly and Padma stretches of the River Ganga, resulting in a relatively sharper snout in specimens from the Ganga than in those from the Narmada. Meanwhile, within the Ganga river, specimens from the Padma stretch, followed by those from the Bhagirathi-Hooghly stretch, possess sharper snouts than specimens from the Middle Stretch of the Ganga. Specimens from the Narmada had deep bodies compared to those from the Ganga, especially from the Padma stretch. A sharper snout and a slender body reduce the drag against currents and facilitate the movement across faster currents and high discharge (Haas et al. 2010; Radkhah et al. 2017).

Interactions of isolation pressure, coupled with local ecological/ habitat dissimilarities and genetic triggers, can lead to adaptive morphometric differentiation in fish populations (AnvariFar et al. 2011; Farook et al. 2013; Mir et al. 2013; Radkhah et al. 2017). Murta et al. (2008) reported a narrower/sharper anterior body region of fish as a response to a faster current and a higher discharge, though other environmental factors may also result in this adaptation. Kumar et al. (2005) reported a higher average annual flow (525.02 km^3 $year^{-1}$) and mean annual discharge (18490 m^3 s^{-1}) in the Ganga, which is way higher than that in the Narmada (45.64 km^3 $year^{-1}$ and 1216 m^3 s^{-1}, respectively). The mean current velocity of the Ganga is also significantly higher (0.97 m s^{-1}) than that of the Narmada (0.22 m s^{-1}). Thus, the relatively sharper snout and the shallower body depth of the Ganga populations of the species might be the result of the adaptation to easy navigation in faster currents and flows in the river. The species exhibited a significantly narrower snout and slender body forms (depth) along the Padma (Beniagram) followed by the Bhagirathi-Hooghly (Nabadwip) stretches, where the mean annual current velocity was faster and discharge was higher. Fish in high-flow habitats have a more streamlined body than those in low-flow habitats (Matt et al. 2017). The difference is not easily perceptible in random specimens; nevertheless, when comparing images of similar size ranges of specimens from different stretches, the difference in snout profile was easily discernible.

Habitat characters influenced the body form of the same fish species from the reservoirs and river habitats differentiated by current and flow characters (Haas et al. 2010; Saemi-Komsari 2021). Environmental variations can result in genetic triggers that manifest in phenotypic expression changes (Melvin et al. 1992). Stream velocity explained variations in morphology of the wild populations of the zebrafish, *Danio rerio* (Shukla and Bhat 2017). The shorter caudal region of the species from the River Ganga populations might be the result of high velocity and flows, as the caudal peduncle of fish in streams having faster flows tends to be more robust (Webb 2015), with larger depth (McLaughlin and Grant 1994). Fish populations from sites with a higher flow velocity tended to have smaller heads, slenderer bodies, and deeper caudal peduncles (Hendry et al. 2006; Haas 2010) and a more fusiform body shape (Jacquemin et al. 2013). Flow velocity exerts evolutionary selection pressure on stream fish morphology (Sánchez-Gonza´lez et al. 2022). However, morphometric variations in stream fishes are strongly linked to more complex ecological, hydrological and evolutionary aspects (Costa and Cataudella 2007; Haas 2010).

Habitat complexity and prey type diversity influence morphological adaptations in fish species (Olsson and Eklöv 2005; Winkler et al. 2017). However, we do not have information on the changes in habitats, food, and foraging modes caused by hydrological variations in rivers to relate these with the morphological changes recorded. Phenotypic differences are also related to local conditions (Langerhans et al. 2003) as well as niche patterns, habitat, resource utilization and behavioural adaptation (Wainwright and Reilly 1994; Eklöv and Svanbäck 2006; Langerhans 2008). Geographical isolation and manmade compartmentalization of rivers result in alterations in habitat, hydrology, trophic structure, etc., leading to changes in resource utilization patterns, behavioural adaptations and selection pressure on fish populations. In the long run, these changes may lead to a change in gene expressions that manifest as the foundation for evolutionary changes in the phenotypic expressions suitable to adapt to the altered environment (Paknejad et al. 2014; Vatandoust et al. 2015). The study highlighted morphometric differentiation between *L. catla* populations of the Ganga and Narmada rivers, and also among those of different stretches of the River Ganga that indicated the existence of different stocks of the species in the river. Information on morphometric changes that are expressed in populations of the species would expand knowledge on possible evolutionary adaptations to hydrological alterations and isolation, which can lead to future studies of morphometric and biological predictors of alterations in environment/ hydrology or environmental flows and ways to mitigate these, besides helping science-based management of fish stocks in the event of altered environmental flows arising out of human interventions. There is a need for ensuring environmental flows and continuity in rivers for the free movement of fish, which needs to be integrated into river modification projects at the conceptual stage itself when any developmental river modifications are envisaged. However, further studies involving morphology, biology, genetics and habitat/ environment interactions are necessary to assess the relative contribution of hydrological characters to these parameters.

Conclusions

Morphometric differences exist between *L. catla* populations of the Ganga and Narmada rivers and among its populations within the Ganga River. The specimens collected from the Ganga have sharper snout profiles, a lesser body depth and a shorter caudal peduncle than those from the Narmada river. Meanwhile, within the Ganga River, the samples from the Padma stretch of the river have the sharpest snout profile and the lowest body depth, which are interpreted as potential adaptations for reducing drag and facilitating navigation in the faster current and high discharge of the river Ganga in general and the Padma stretch of the river, in particular. Based on these characteristics, the populations of the species distributed along the middle stretch of the Ganga, the Bhagirathi-Hooghly and Padma stretches can be considered as three distinct stocks mediated by hydrological difference and isolation. This can be the basis for the stock-specific fisheries monitoring and management of the species in rivers.

ACKNOWLEDGEMENTS

We thank Dr K.K. Vass and Prof. A.P. Sharma, former Directors of ICAR-Central Inland Fisheries Research Institute, Kolkata for providing the necessary facilities to carry out the study and the present Director Dr B.K. Das for clearing this manuscript for communication. We also thank the Technical Officers and Support staff of ICAR-Central Inland Fisheries Research Institute, Kolkata and its Regional Centre at Allahabad, who assisted in sample collection and handling. The study was part of the first phase of ICAR-Outreach Activity on Fish Genetic Stocks (No. OR/ER/08/09/002).

Competing interest

The authors have declared that no competing interests exist.

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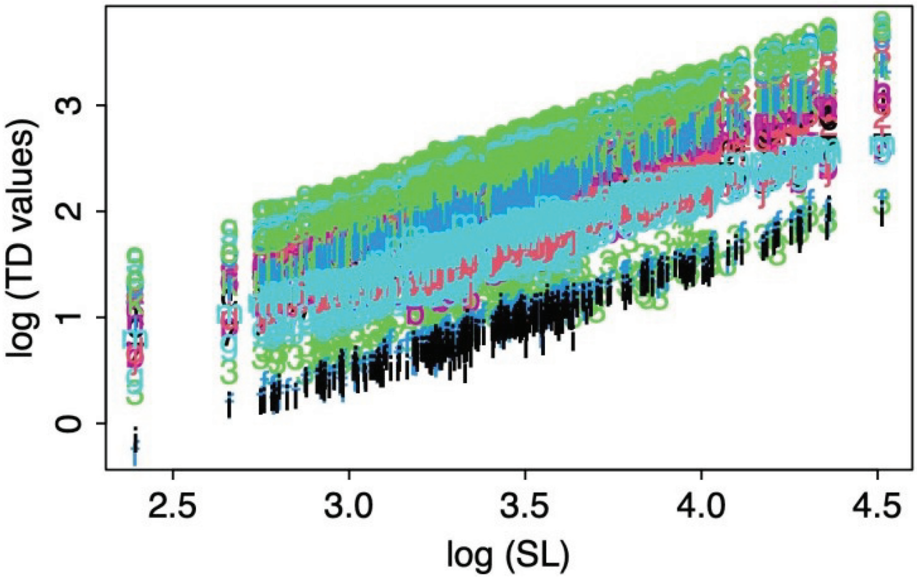
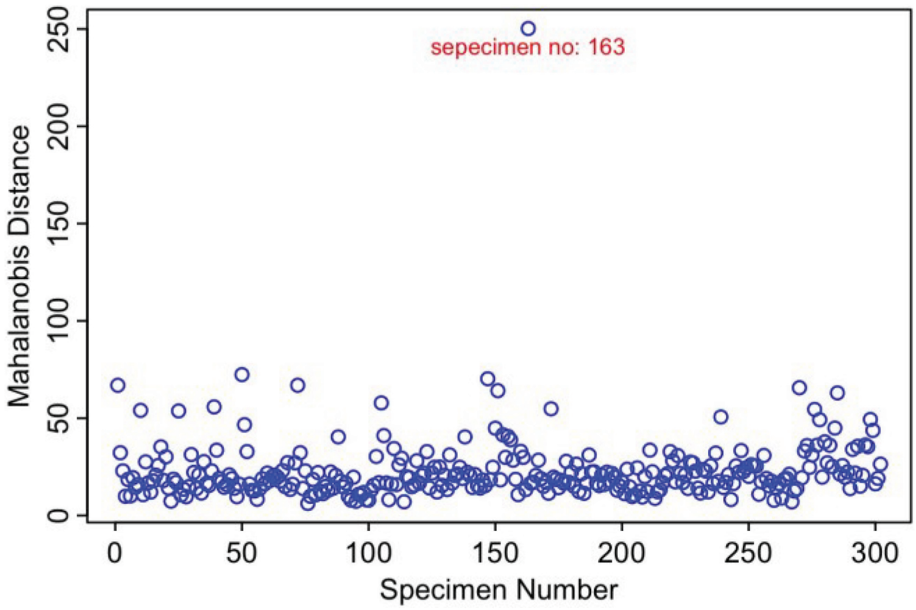
SUPPLEMENTARY FIGURES AND TABLE



Supplementary Figure 1. Log-log scatter plot of TD measurements and SL for all samples. TD: Truss Distances in cm; SL: Standard Length in cm.



Supplementary Figure 2. Outlier detected from the data set using the Mahalanobis distance measure (specimen no. 163.)

Supplementary Table 1. Results of Tukey HSD test for pair-wise comparison of head shape.

Pair	Difference	95% lower bound	95% upper bound	*p*-value
Beniagram- Ganga_Middle	-3.935	-4.546	-3.324	<0.001
Nabadwip- Ganga_Middle	-2.384	-3.000	-1.768	<0.001
Narmada- Ganga_Middle	1.31	0.508	2.111	<0.001
Nabadwip-Beniagram	1.551	0.861	2.24	<0.001
Narmada-Beniagram	5.244	4.386	6.103	<0.001
Narmada-Nabadwip	3.694	2.831	4.556	<0.001