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On the morphological variations of geographically isolated migratory and non-migratory populations of Tropical shad, *Tenualosa ilisha* (Hamilton, 1822) from three distinct tropical ecosystems

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The migratory tropical shad, *Tenualosa ilisha* has a wide range of habitat preferences like rivers, reservoirs, estuaries, backwaters, and coastal waters during different phases of its life cycle. The present study investigates morphological variations among three populations of Hilsa from distinct ecosystems such as the River Brahmaputra, Narmada estuary and Ukai reservoir. Thirteen morphometric and nine meristic measurements were considered for the present study. Among the meristic traits, significant variation was observed in counts of lateral line scales and post ventral scutes. The MANOVA results depict a significant difference in the morphometric traits among the three populations. The factor analysis indicated a very significant loading of head-related traits on the first factor and traits related to the middle and caudal region on the second factor. The study portrayed a significant morphological variation among the different stocks of *T. ilisha* and the results were confirmed in discriminant function analysis.

[**Keywords**: Distinct location, Geographically isolated population, Meristic traits, Morphometric traits, *Tenualosa ilisha*]

Introduction

Tenualosa ilisha (Hamilton, 1822), commonly known as Hilsa shad or tropical shad is an anadromous clupeid, with a wide distribution range from the Persian Gulf eastward to Myanmar, including Western and Eastern coasts of India[1]. Hilsa shad substantially provides a livelihood to millions of people throughout India, Bangladesh, and Myanmar, which implies its immense commercial importance and high market demand[2]. The global annual average catch of Hilsa is about 0.72 million tons, of which the contribution of India is about 15-20 %, i.e., about 0.11-0.15 million tons[3]. The euryhaline shad population predominantly inhabits a broad geographical range of ecologically distinct habitats like rivers, estuaries and coastal waters of Southern Asia[4]. A prominent migration of this anadromous shad occurs during the monsoon season, as the school of species ascends to the freshwater zones of rivers from the coastal waters for spawning and forms a lucrative catch in the inland waters[5]. In India, the migratory Hilsa population is mainly spotted in major rivers like Ganga, Brahmaputra, Godavari, etc. along the east coast and from the rain-fed peninsular rivers like the Narmada, Tapti, etc. along the west coast and its conjoined tributaries, backwaters, and estuaries[1]. In addition to this, a non-migratory population of Hilsa was divulged from a substantially lacustrine ecosystem of the Ukai (Vallabhsagar) reservoir in the Gujarat state of India[6].

Ecologically distinct habitat preferences are evident in these migratory shad populations, which use river-estuary systems and coastal waters during different phases of its life cycle. The broad range of habitat preferences in geographically isolated populations of migratory species may impart morphological variations, in response to selection pressure from diverse local ecological regimes[7]. The morphological characteristics of the organisms respond to the environmental parameters and these biotic-habitat interactions shape suitable functional phenotypic traits[8]. The traits that molded gradually with these interactions enable organisms to suit and survive in a particular ecosystem. The variations due to eco-morphological interactions may be farther escalated by the loss of dispersal and gene flow between distinct migratory populations[9].

Hence an exhaustive study on the morphology of geographically isolated migratory species may reveal the phenotypic distinction carved out by the ecological interactions. Moreover, this sort of studies on morphological variations also facilitates a greater understanding of the ecological conditions in the system where the species exists[10].

The meristic and morphometric characteristics of fish species are two major features that are enormously used for the studies on intraspecific morphological divergences[11] and are sound tools in stock structure studies for fisheries management purpose[12]. As a commercially important fish species, a wide array of studies was conducted to study the stock structure of the Hilsa population distributed along the Indian subcontinent for designing suitable management plans, but such studies were mainly concentrated in the state of West Bengal[13]. Furthermore, the investigations on the population genetic structure delineate two distinct populations of Hilsa in the Bay of Bengal and Arabian sea by analyzing the variations in mitochondrial DNA sequences[14]. The earlier morphological investigations on Hilsa in India were summarized with a chance in the occurrence of different phenotypic stocks in Indian rivers[1]. While more statistically sound investigations on morphological variations, among the geographically distinct populations of Hilsa across the country, are meager. It is imperative to know about the extent of morphological changes happened to the shad populations in its geographical range of occurrence and thereby to develop suitable management measures. The present study was performed to investigate the possible morphological variations in the geographically isolated populations of Hilsa from three distinct tropical ecosystems *viz*. Brahmaputra river (a snow-fed perennial river), Narmada estuary (an estuarine system) and the Ukai reservoir (a lacustrine ecosystem).

Materials and Methods

Study area

Samples of *T. ilisha* were collected from three locations (Fig. 1) *viz*., Guwahati and Dhubri stations of Brahmaputra river in Assam; Bhadbhut and Jhanor stations of Narmada estuary in Gujarat and from Ukai Reservoir in Gujarat (Table 1). Brahmaputra river, snow-fed perennial Himalayan river flowing in the north-eastern part of India and drains into the Bay of Bengal, after covering a distance of about 918 km in India[15]. The Brahmaputra river valley in Assam is characterized by diverse hydro-ecological characters, with width varies from 64 km to 94 km and about 640 km long and the river is devoid of any tidal influences[16]. The Narmada estuarine system is located at the Bharuch district of Gujarat, formed after the confluence of Narmada river with the Arabian Sea at Gulf of Khambhat and the total estuarine area is about 14,250 ha[17]. This tropical estuarine system is characterized by a more pronounced nutrient dynamics and hydro-ecological changes in the system were determined by the river water inflow and varying tidal amplitude[18]. The funnel-shaped estuary is characterized by the semidiurnal tide and the migration of Hilsa in the estuary happens mostly during the South-West monsoon season. The Ukai reservoir (submerged area- 51,520 ha), a total lacustrine ecosystem located in river Tapti at the

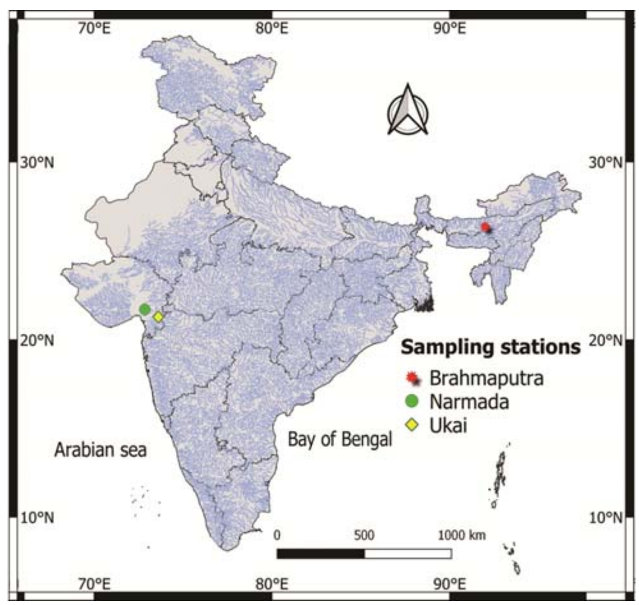

Fig. 1 — Map showing the details of sampling stations

Table 1 — Details of sampling stations and fish sample

Source of fish sample	Type of ecosystem	Location	Period of sampling	Sample size	Mean TL ± SE (cm)
Brahmaputra	Riverine zone	26°19′15″N 91°75′60″E	Sep 2017 - Dec 2018	91	26.1 ± 0.54
Narmada	Estuarine zone	21°40'52"N 72°50'42"E	Jul 2018 – Feb 2019	95	28.2 ± 0.56
Ukai	Reservoir	21°16'32"N 73°36'24"E	Jan 2018 to Feb 2019	74	18.5 ± 0.34

Gujarat state and the reservoir has a distance of about 250 km from the Narmada estuary[6].

Sample collection

A total of 260 specimens of Hilsa shad were collected from the commercial catches during the study period (Table 1). Only intact specimens were selected from the catch and transported to the laboratory after discretely chill packed with sufficient ice in an insulated fish box, for further analysis.

Data collection

In the laboratory, the specimens were digitized on a laminated graph sheet using Sony DSC W830 (20.1 MP Camera), keeping the left side up. For the elicitation of morphometric measurements from images three software's were used namely; tpsUtil – to convert the images into tps format[19]; tps Dig V2.1- for the digitization of landmarks on the image[20] and PAST- to extract the morphometric measurements from the predetermined landmarks[21]. The extraction of the morphometric measurements using the image processing techniques is widely accepted as it helps to reduce the time taken in the field collection of data[22].

Thirteen morphometric and nine meristic measurements were recorded for further morphological variation studies (Fig. 2). The morphometric measurements recorded are: TL-Total length; SL-Standard length; FL-Fork length; HL-Head length; ED-Eye diameter; PROBL-Pre-orbital length; POOBL-Post-orbital length; PDL-Pre-dorsal length; PPECL-Pre-pectoral length; PVL-Pre-ventral length; PAL-Pre-anal length; BD-Body depth and CPD-Caudal peduncle depth (Fig. 2). The selected meristic counts are; DR-Dorsal fin rays; PR-Pectoral fin rays; VR-Ventral fin rays; AR-Anal fin rays; PrVSc-Pre-ventral scutes; PoVSc-Post-ventral scutes; BSR-Branchiostegal rays; LL-Lateral line scales and CR-Caudal fin rays.

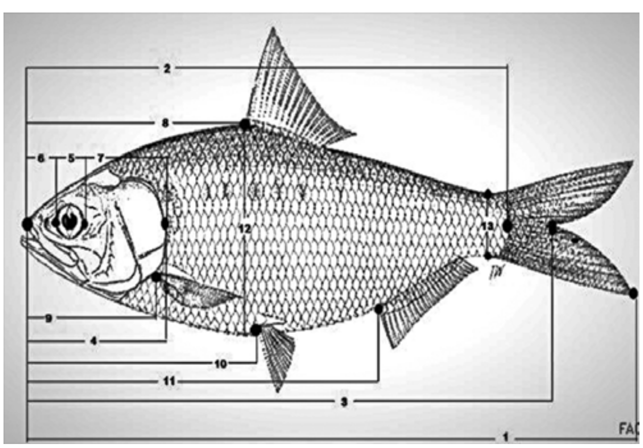

Fig. 2 — Image (adopted from FAO) illustrating the morphometric traits such as: 1-TL; 2- SL; 3-FL; 4-HL; 5- ED; 6-PROBL; 7-POOBL; 8-PDL; 9- PPECL; 10-PVL; 11-PAL; 12-BD and 13- CPD

Statistical analysis

Fishes are known to have the allometric growth and the size-dependent variation was removed by using the formula (Elliott *et al*.[23])

$$M_{adj} = M\,(L_s/L_0)^b$$

Where, M is the original measurement, M_{adj}-the transformed measurement, L_0-the standard length of the fish, L_s- the overall mean of standard length for all fish from all samples in each analysis, and b estimated for each character from the observed data as the slope of the regression of log M on log Lo using all fish from each group. Further, the normality of the log-transformed variables was tested and a total of twenty outliers were removed. The correlation coefficients calculated between the size-corrected variables and standard lengths were found to be non-significant, hence the data transformation successfully removed the size effect in the variable. Multivariate Analysis of Variance (MANOVA) was used to find the significant difference between the three populations of Hilsa. Factor analysis with Maximum likelihood method was performed to find the morphometric variables responsible for differentiating the fish populations location-wise, System wise (Lotic system of Narmada estuary and the Brahmaputra river; Lentic system of Ukai reservoir) and Coastwise (Brahmaputra river in the East coast and Narmada estuary from the West coast). As Ukai is a lacustrine ecosystem, it is not included while analyzing the Coastwise morphological variations. The factors with a loading score of more than 0.30 are considered as significant, > 0.40 is more significant, and loading scores of 0.50 and above are considered very significant[24]. Hence in this present study factors, more than 0.7 are considered for further analysis. The discriminant function analysis was then conducted to predict or classify each specimen to their respective locations, using the selected morphometric traits with a very significant loading in the factor analysis. Kruskal-Wallis non-parametric test was employed here to statistically confirm the variations in the selected meristic traits of Hilsa between the locations. Statistical analyses for morphometric and meristic data were performed using the STATISTICA V.8 software package[25] and Excel (Microsoft Office 2016).

Results

Analysis of meristic traits

Differentiation in the meristic characters between the three locations was tested using the Kruskal-Wallis test. The Kruskal-Wallis analysis results indicated that among the nine meristic characters chosen, only two characters *viz.* lateral line scales and post ventral scutes are depicting a significant difference between the locations (Table 2).

Analysis of morphometric traits

The multivariate statistical analysis of morphometric measurements was performed after removing the size-dependent variations on the variables. The MANOVA results helped to disclose the significant morphological variations between the three populations of Hilsa ($p < 0.05$). In factor analysis, the variables with a highly significant loading (loading > 0.7) are only considered as it considerably accounts for the variations. For the location wise factor analysis, the first factor (Factor 1) accounted for 42 % and the second factor (Factor 2) accounted for 29 % of the variation (together accounted for 71 % of the variation). The morphometric measurements related to the head region indicated a highly significant loading on the first factor and the variables on the middle and caudal peduncle region like BD, PAL, and CPD showed a very significant loading in second factor (Table 3). The highest loading is observed for HL in comparison to other variables. Spatial variations in the morphology of fish populations with locations are exemplified in the scatter biplot (Fig. 3). The bi-plot portrays that the three populations were separated along the horizontal axis, showing the more significant contribution of the first factor in deciphering the populations.

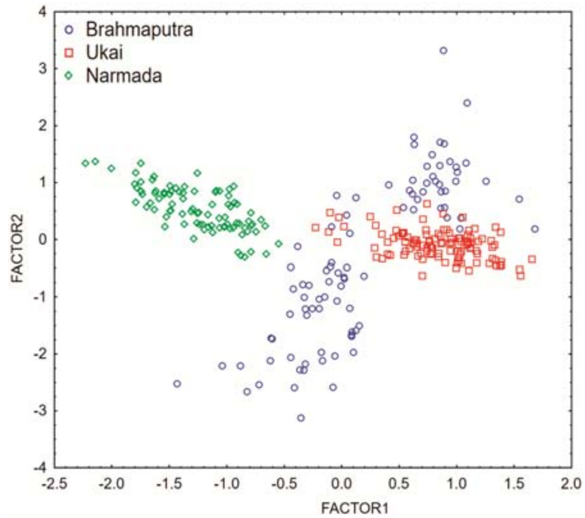

Fig. 3 — Scatter plot of factor 1 and factor 2 obtained from morphometric measurements showing the location-wise morphological differentiation

Table 2 — Details of Kruskal-Wallis test results of meristic traits

Meristic traits	Kruskal Wallis test (H-Value)	P-value
DR	2.01	0.33
PR	1.65	0.43
VR	2.46	0.29
AR	2.78	0.56
PrVSc	.143	0.93
PoVSc	7.62	0.02*
BSR	0.00	1.00
LL	204.10	0.00*
CR	0.00	1.00

Table 3 — Factor loadings for the morphometric parameters showing the location-wise, system-wise and coast-wise variations

PARAMATERS	LOCATION-WISE		SYSTEM-WISE		COAST-WISE	
	Factor 1	Factor 2	Factor 1	Factor 2	Factor 1	Factor 2
HL	0.970963	0.193424	0.971738	0.183402	0.966538	0.202194
ED	0.845678	0.004963	0.845654	-0.003049	0.754553	0.000694
PROBL	0.592071	0.212539	0.569004	0.155333	0.923631	-0.123374
POOBL	0.883036	0.177269	0.894339	0.187185	0.774386	0.374860
PDL	0.792928	0.517127	0.787509	0.498482	0.897746	0.375470
PPECL	0.103488	0.027514	0.139896	0.100286	-0.664787	0.593171
PVL	0.704543	0.657596	0.704433	0.646926	0.808480	0.545845
PAL	0.354049	0.928385	0.362559	0.912529	0.556641	0.816234
BD	-0.119329	0.828481	-0.102063	0.866330	-0.040224	0.941537
CPD	0.329584	0.715553	0.331503	0.726508	0.486370	0.666611

The system-wise (lotic and lentic) variations were also checked and the factor analysis results are the same as that obtained in the location wise analysis (Table 3). The coastwise factor analysis illustrates that the first factor accounted for 52 % of the variation and the second factor accounted for 30 % of the variation. Noticeable variation was observed in the scatter plot with the separations that happened along the vertical axis, indicating the contribution of the second factor in the separation of two populations (Fig. 4). Significant loading was observed for the body depth on the second factor and the traits related to the head region (HL, ED, PROBL, POOBL, and PDL) exhibit a very significant loading in the first Factor.

Discriminant function analysis

The results of location wise morphometric variations in the factor analysis are cross-validated using the discriminant function analysis to analyze the extent of similarity between the samples collected from different locations (Table 4). In the cross-validation analysis, the well-classified group is that of the Narmada estuary with 100 % well classification to the station. The overall successful classification rate obtained in the analysis is about 98 %.

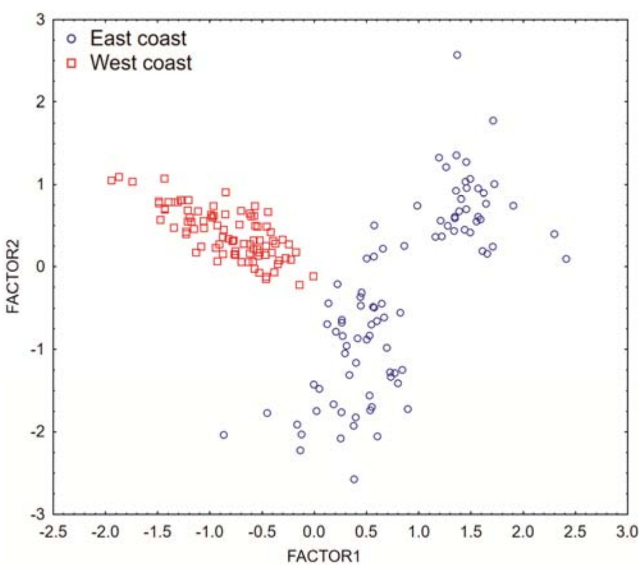

Fig. 4 — Scatter plot of factor 1 and factor 2 obtained from morphometric measurements showing the Coast-wise morphological differentiation

Discussion

A significant morphological variation is undoubtedly pointed out, for the first time, in three geographically isolated populations of *T. ilisha* from Brahmaputra river, Narmada estuary and Ukai reservoir during the present study. Amongst the nine meristic characters in comparison, a compelling variation was brought up only in two characters *viz.* lateral line scales and post ventral scutes. The results of MANOVA signaled a significant difference in three populations of Hilsa from different locations. The factor analysis results pointed out the morphometric parameters which are significantly contributed to deciphering the three populations of the species. It is further corroborated in discriminant function analysis (DFA), where 98 % of the individuals are successfully classified into the respective locations. A higher well classification rate indicates more distinctness in the samples and which depicts a significant geographical separation between fish stocks[26].

Meristic counts in the fishes are liable to changes in the environmental conditions, to which the organism is exposed during the early developmental stages[27]. The diverse environmental conditions (mostly temperature, dissolved oxygen, and salinity), experienced by the isolated populations of the same species in the later growth phase also inflict further variations in count[28]. Though the meristic traits are less susceptible to ecological alterations, a considerable variation is evident in fish populations from distinct geographical locations[29]. The combined effect of multiple parameters mainly hydrodynamic changes, diverse feeding habits, developmental constraints, etc. are capable of creating significant alterations in the meristic traits like lateral line morphology[30].

Table 4 — Cross-validated classifications from Discriminant function analysis: given the number of observations and the percentage classification (in paranthesis)

Location	Brahmaputra	Narmada	Ukai	Total
Brahmaputra	90 (98.9)	0(0)	1 (1.1)	91
Narmada	0(0)	95 (100)	0(0)	95
Ukai	4(5.4)	0(0)	70 (94.6)	74
Total	94	95	71	260
Total success classification rate: 98 %				

Factor analysis of morphometric traits depicted a very significant loading in the head region (HL, ED, and POOBL) and the traits related to the middle and caudal region of fish. The factor analysis results of the lotic and lentic systems also indicated the same result as above. A scatter plot on the coast wise analysis of morphometric variations including the samples from Narmada estuary and Brahmaputra river revealed that the separation between the two stocks is more significantly attributed to body depth in comparison to other traits related to the anterior region of the body. The coastwise variations were more probably caused by variations in the regional environmental parameters and geographical conditions, due to a wider longitudinal separation between the coasts[12]. The previous studies on the ecology of Narmada estuary and the Brahmaputra river clearly portrayed the distinctness in environmental and geographical conditions of this two aquatic ecosystems[16-18]. Moreover, the extent of the geographical separation is mentioned as a major force in molding the phenotypic stocks in aquatic ecosystems[26].

The variations in body depth may be attributed to the need for the maintenance of balance and efficiency in changing water flow conditions. Fusiform body in swiftly flowing water helps the fish to sustain the drag in comparison to the deeper bodied morphology in the low flow or the lentic ecosystem[31]. Further, the existence of 'fat' and 'thin' morphs of Hilsa was reported from Bangladesh waters[32]. The Brahmaputra river on the east coast has a diverse regime of flow pattern, physico-chemical parameters and habitat structure in comparison to Narmada estuary on the West coast[15-18]. Hilsa population from the Ukai reservoir is completely adapted to an impounded habitat, with a significant alteration in its growth rate and behavior compared to the migratory stock of Hilsa in the lotic habitat[6]. The changes in hydrological conditions, such as the variation in flow rates due to impoundments, etc., may also cause morphometric variations in fishes mainly on the head size and positions of fins and eyes[33,34]. Alterations in the feeding pattern of fish species in distinct ecosystems and changes in predatory organisms may also impart significant morphometric variations especially on traits related to head region such as head length, eye diameter, eye position etc.[35]. *T. ilisha* is a planktivorous fish with filter-feeding behavior, while a significant variation on the feeding habits with the season, ecological conditions, presence of food substance in the habitat, etc., were widely reported in this migratory fish species[36-38]. The changes in the quality and abundance of food in the ecosystem significantly influences the body morphology of fishes[27,39]. Moreover, it was opined that the morphological variations that happened to fish species in a different habitat, maybe occurred due to a correlated effect of multiple environmental factors rather than having the specific effect of one or two factors[40].

Diverse ecological conditions at distinct aquatic habitats were pointed out as a major reason for the morphological variations in different stocks of the same fish species[41]. Morphological variations are gradually molded-in geographically isolated populations, as a need for adaptation in diverse ecological regimes[42] and which may not necessarily require a genetic distinctness[43]. These crucial variations acquired through behavioral adaptation enables the fish populations to sustain in a particular environment[7]. Even an ample morphometric variation is evident in the genetically homogeneous population of Hilsa in Bangladesh, emphasizing the influence of the local environmental conditions in the formulation of phenotypic stocks[44].

The local ecological interactions or genetic divergence or the combined effect of both factors may be a reason for the morphological variations in geographically distinct populations. The more clarity in this aspect can be acquired with an in-depth study by correlating the local and regional physico-chemical parameters with the functional phenotypic traits of organisms, backed up with sufficient biochemical or molecular analysis. The molecular analysis can further elucidate the extent of variation imparted between the populations due to the genetic divergence. The present investigation proved morphological variations among the geographically isolated population of *T. ilisha* in inland water bodies in India. The changing global climate conditions and the increased anthropogenic impacts cause serious alterations to aquatic habitats and which may lead to the modification of phenotypic and behavioral traits of geographically distinct populations of migratory fishes like Hilsa. An extensive study along the wider geographical range of Hilsa is henceforth necessary to gather more detailed information on the extent of morphological variations that happened due to the adaptive cue and thereby decipher its stock structure for the management purpose.

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Conflict of Interest

The authors declare that they have no known conflict of interests.

Author Contributions

GV: Writing manuscript, data collection and conception of idea and design; SB: Substantively revised the manuscript, helped in data collection from Brahmaputra river, manuscript designing and interpretation of data; GD: Drafting and revising the manuscript; AKJ and AKS: Designing the study, critically revised the manuscript; MS: Statistical analysis, interpretation of results and creating GIS map; VN: Sampling survey, collection of samples and laboratory works; GB: Sampling survey, collection of samples, data collection, analysis of taxonomic data, digitization of samples, etc.; BKD: Conception of idea, designing the manuscript and final critical revision of the manuscript.

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