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Reproductive vulnerability of *Tenualosa Ilisha* in the river Ganga: a climate-driven challenge

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Abstract

The maturation and spawning of fish in riverine systems are closely influenced by hydro-climatic conditions, particularly in major river such as the Ganga. The present study investigates the impact of climate change and environmental factors on the reproductive biology of Hilsa shad (*Tenualosa ilisha*) in the Farakka region of the River Ganga. The results indicated that Gonadosomatic Index (GSI) values for both male and female specimens peaked during the early winter months (November to December), followed by a steady decline. This trend suggests that spawning most likely takes place in late November or early December. Rainfall (RF) showed a statistically significant positive correlation with GSI during the pre-monsoon and monsoon seasons ($p < 0.05$), whereas air temperature (AT) exhibited a negative influence during the monsoon and post-monsoon periods. Furthermore, the Generalized Additive Model (GAM) indicated a strong, non-linear yet positive relationship between water temperature and GSI values, particularly within the range of 25–28 °C. This study presents novel insights into how environmental variables influence the reproductive capacity of *T. ilisha* in the River Ganga.

Keywords River ganga · Gonadosomatic index · Climate change · Conservation · Environmental factor

1 1. Introduction

The River Ganga, one of India's most significant river systems, originates from the Gangotri Glacier in the Garhwal Himalayas at an elevation of approximately 4,100 m above sea level. The river commences as the 'Bhagirathi' in the Uttarakhand region, and after gorging down for about 205 km, it joins the River Alaknanda at Devprayag, where it officially takes the name Ganga (Jain et al., 2007). As the Ganga runs in between the Indian territories of Uttarakhand, Uttar Pradesh, Bihar, and West Bengal, it is joined by several tributaries, the most prominent of which are the Ghaghara, Yamuna, Kosi, Gandak and Son. These rivers

Extended author information available on the last page of the article

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greatly influence the river's volume and hydrological dynamics. The Ganga sustains a variety of habitats along its path, giving habitat for a diverse range of aquatic animals such as freshwater fish, amphibians, and the endangered Gangetic River dolphin (Tandon & Sinha, 2018). The fish diversity in the Ganga River is substantial, reflecting the varied ecological conditions along its course. Fish species range from cold-water regimes in the upper reaches to warm-water in the plains. Recently, Das et al. (2023) have reported a total no. of 190 fish species belonging to 133 genera from the entire stretch of River Ganga, ranging from Harsil (Uttarakhand) to Fraserganj (West Bengal). Among all the notable fish species, Hilsa (*Tenualosa ilisha*) is the most iconic and commands great economic and cultural significance in the lower part of the River Ganga.

Hilsa shad, *Tenualosa ilisha* is a highly exploited euryhaline fish of River Ganga. The species is widely distributed in Indian subcontinent and as well as in Myanmar, Sumatra, Indonesia, Iran, Iraq, Kuwait and Vietnam (Talwar & Jhingran, 1991). The species mainly inhabits the Arabian Sea, Persian Gulf, Indian Ocean, Bay of Bengal, coastal water, estuaries and freshwater rivers (De, 1980). Hilsa fishery supports the livelihood of huge number of people who are directly or indirectly connected to this single species fishery (BoBLME, 2012; Wahab & Beveridge, 2019; Rahman et al., 2020). Hilsa is highly regarded in West Bengal, Odisha, Bangladesh, and the northeastern Indian states due to its distinctive flavour and its socio-cultural and religious significance. According to research, Bangladesh is the leading producer of Hilsa, with 86% of the production coming from untamed rivers while India follows with 8%, Myanmar has 4%, and the remaining 2% is produced by other Hilsa-producing nations (Bhaumik, 2013a; Roy et al., 2016; Rahman et al., 2018). Recent assessments indicate a steady decline in wild Hilsa catches across major river systems, including the Ganga-Brahmaputra delta, largely due to overfishing, juvenile exploitation, and climate variability (FAO, 2022; Islam et al., 2020). As Hilsa fisheries form part of shared aquatic resources between India and Bangladesh, both countries have been engaged in regional cooperation initiatives under the Bay of Bengal Programme (BoBP) and South Asia Cooperative Environment Programme (SACEP) to promote sustainable management practices (Aftabuddin et al., 2021). These include seasonal fishing bans, minimum mesh size regulations, and community-based management approaches. However, enforcement remains a challenge due to socio-economic dependence and inadequate monitoring frameworks.

Apart from rich health benefits (Hossain et al., 2014; Ganguly et al., 2018), hilsa consumption increases immunity which leads to prevention of many human diseases (Sidhu, 2003). The Hooghly River in India offers the most extensive breeding grounds along its riverbed, where hilsa migrate biannually from the sea to complete their life cycle (Jones & Menon, 1951). The utilization of modern vessels and equipment, particularly trawlers employing long monofilament and multifilament gill nets, obstructs the brooder hilsa from performing their reproductive cycle, resulting in decreased catch from the rivers of India and Bangladesh in recent years (Suresh et al., 2017; Wahab et al., 2019).

Investigating reproductive biology is one of the fundamental necessities for understanding a species life cycle, its profit potential, and conservation efforts. Since fish reproductive parameters and maturity are commonly evaluated for management and evaluation, they serve as a practical and cost-effective way to differentiate between stocks (Morgan, 2008). The annual egg output of female fish, known as fecundity, plays a significant role in assessing population dynamics and levels of exploitation (Lambert, 2008). The gonadosomatic index, or GSI, is employed to assess ovary readiness and the development stage of gonads, revealing the current stage of the reproductive cycle (Jan et al., 2014; Chaubey et al., 2021).

A rise in the global surface temperature of +0.99 °C was observed during the last two decades of the 21 st century, which span from 2001 to 2020 (IPCC, 2021). The climatic trend in India has demonstrated that several main river basins are experiencing different scenarios. According to the report published by the Indian Meteorological Department (IMD), the average air temperature in the lower Gangetic plains of the Indian subcontinent has increased by a range of 0.20 to 1.2 °C (with a mean rise of 0.62 °C), while the total annual rainfall has decreased by a range of 135.6 to 257 mm (with a mean decrease of 192.5 mm) over the past four decades (1981–2020) (Sarkar et al., 2017, 2021c). Climate change has wide-ranging impacts on aquatic environments, significantly affecting natural-water fisheries, fish assemblages and stocks, species distribution, and fisheries management organizations in various ways (Cheung et al., 2013). Climate change factors, like increased water temperature and irregular rainfall, have increased stress on natural ecosystems, altering their equilibrium and considerably diminishing their ability to recover and remain resilient. As a result, ecosystems are becoming more sensitive to external stressors such as extreme weather events, habitat degradation, and biodiversity loss, making it more difficult for these environments to recover and continue performing their natural roles. This lower potential for recovery has an impact not just on ecosystems but also on the species and populations that rely on them for life and well-being (Adger et al., 2005; Lebel, 2013). In addition, extreme climatic and environmental conditions may lead to early maturation and spawning in the natural waters and shorter life spans (Sutherland et al., 1986; Arula et al., 2017). Although numerous studies have addressed Hilsa migration and breeding in relation to seasonal monsoon cycles, there is limited research that directly correlates long-term climatic variables with reproductive maturity indices. Given the interannual and decadal variability observed in riverine ecosystems, it is essential to adopt integrative approaches that consider hydro-climatic feedbacks and their ecological consequences (Avinash & Dwarakish, 2023). This is particularly important in the context of adaptive fisheries governance under climate uncertainty.

The methodological innovation of this study lies in the integration of empirical, field-based reproductive biology data collected over three years (2021–2023) with long-term meteorological records spanning 38 years a rare and underutilized approach in Hilsa research within the Indian subcontinent. This comprehensive temporal framework allows for a robust investigation of climate-driven biological responses. Furthermore, the application of a Generalized Additive Model (GAM) represents a novel analytical advancement in this domain, enabling the modelling of complex, non-linear relationships between multiple hydro-climatic variables and the Gonado-Somatic Index (GSI) of Hilsa.

Unlike previous studies that have typically examined reproductive traits or water quality parameters, our GAM-based approach provides a flexible, data-driven framework that systematically links environmental drivers to reproductive maturity. This allows for a more nuanced understanding of how climatic variability, such as temperature shifts and rainfall anomalies, may contribute to early gonadal maturation and altered breeding phenology in Hilsa. By linking long-term climatic trends with reproductive dynamics, this study offers not only the ecological insights into species-environment interactions but also a quantitative decision-support tool for guiding adaptive fisheries management and climate-resilient conservation strategies in the Ganga River ecosystem.

2 Materials and methodology

2.1 Study area and collection of specimens

The Farakka Barrage, constructed in 1975 on the River Ganga in India, serves as a significant strategic international location. River Ganga in Farakka is divided into two arms, channelized into both India and Bangladesh. The barrage was constructed to provide freshwater to the Kolkata port, which experienced drought during the dry season. The construction has considerably hindered the upstream migratory movement of Hilsa fish. Before its construction, Hilsa migrated up to Prayagraj via the Ganges for spawning. Over the past three decades, from 1990 onwards, faulty fish passes have further obstructed the Hilsa migration, causing near-complete depletion of the species upstream of the barrage. However, availability of Hilsa is abundant in the lower side of the barrage throughout the year, with sporadic availability during March to June. The decline in the upper reaches of the dam has adversely affected biodiversity, the livelihoods of fishermen in the adjoining areas.

In the present study, 1834 *T. Ilisha* specimens (864 males and 970 females) ranging from 60 to 363 mm (total length) and 13–603 g (body weight) were collected from River Ganga (24.8040° N and 87.9322° E) at Farakka, Murshidabad, West Bengal (Fig. 1). The sampling of fishes was conducted monthly from January 2021 to December 2023 and was obtained from the early morning catch of the river using gill nets (mesh size: 50–110 mm) and also from local commercial landing sites.

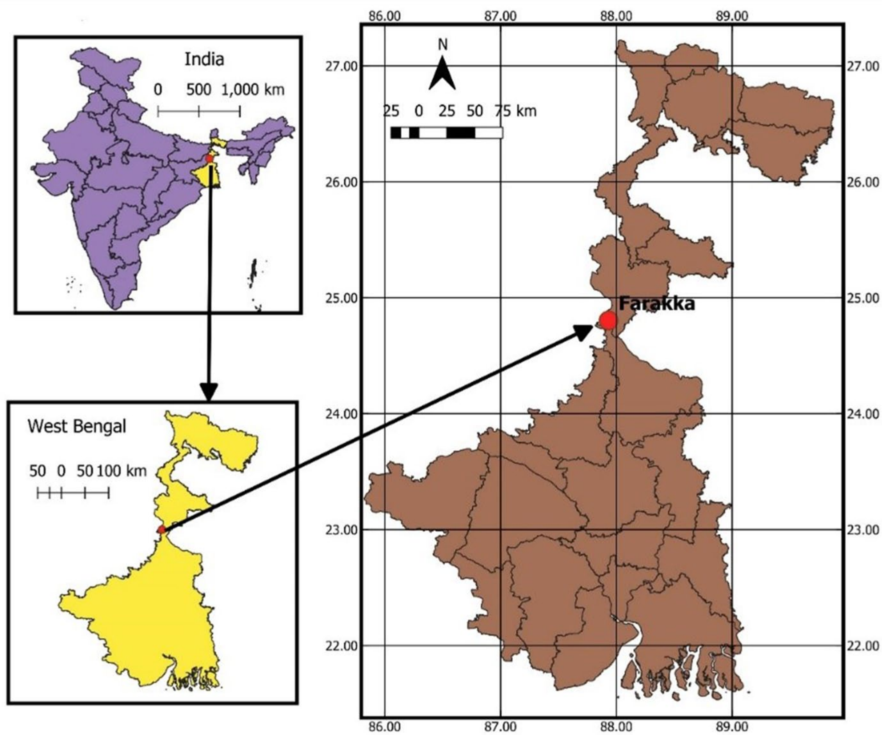

Fig. 1 The map depicting the study area in River Ganga, West Bengal

2.2 Estimation of reproductive biology parameters

The fresh specimens of Hilsa were transported from the collection sites in ice-preserved condition (4 °C) in an insulated container within twenty minutes of capture. The total length and body weight of each fish specimen were measured to the nearest 0.1 mm and 0.01 g, respectively. Each fish was dissected to check the maturity status and the gonads were measured to the nearest 0.001 g using a sensitive electronic balance (Scout pro SP402, Ohaus Corporation, USA). Subsequently, the gonads were preserved in a separate dry container in 10% formaldehyde solution (HiMedia Laboratories) for further use.

2.3 Fecundity and gonado somatic index

Three typical sets of sub-samples were removed from the front, middle, and posterior regions of the ovary, and the fecundity was estimated using the gravimetric method (Murua et al., 2003). After removal of formalin from the ovarian surface using a tissue paper, tiny segments of the ovary, approximately 2 mm in length, was cut and weighed to the nearest 0.001 g. After being separated with a needle, the oocytes were examined and counted with a stereomicroscope (Zeiss Stemi 2000-C). The Gonado-Somatic Index (GSI) was computed monthly using the formula GSI= (Gonadal Weight)/(Total Body Weight) × 100. The cumulative proportion against total length (mm) was depicted as the size at first sexual maturity (Lm), which was determined by measuring the length at which 50% and 25% of the population were found to be mature (Bhakta et al., 2021).

2.4 Water quality parameter

River water samples were taken monthly in triplicate from the site in pre-washed plastic bottles. The chemical parameters viz. dissolved oxygen (mgL^{-1}), free carbon dioxide (mg L^{-1}), total hardness (mg L^{-1}), total alkalinity (mg L^{-1}), nitrate (mg L^{-1}) and available phosphate (mg L^{-1}) were analysed by titrimetric method following the standard methods of APHA, 2017. The standard physical water quality parameters like atmospheric temperature (°C), water temperature (°C), pH, salinity (ppt), total dissolved solid (mg L^{-1}) and electrical conductivity (μS/cm^{-1}) were analysed on the spot immediately after collection using a multi-digital probe (YSIPRO DSS). Water transparency was measured by using a Secchi disk (Strickland & Parsons, 1972).

2.5 Climatic analysis

The analysis methodologies for the last three decades of normal data were employed to examine the climatic changes in the current study. The monthly climate data (mean air temperature and annual rainfall) for the 38 years from 1985 to 2023 for the Murshidabad district in West Bengal was obtained from the Indian Meteorological Department (IMD), Kolkata, India. A simple linear trend analysis was conducted to ascertain the long-term trend.

2.6 Statistical analysis

The simple descriptive statistics, such as the mean, standard deviation, minimum, and maximum values, were calculated using Microsoft Excel 2010. Karl Pearson correlation analysis was performed to explore relationships between reproductive parameters and environmental variables. Additionally, the Generalized Additive Model (GAM) was fitted using the "mgcv" package in R (R-4.4.2).

2.7 Model derivation

Generalized additive model (GAMs) To explore the non-linear relationships between water quality variables and the response variable, i.e. the GSI, more comprehensively, the Generalized Additive Model (GAM) was utilized. GAM build upon the Generalized Linear Model (GLM) by incorporating smooth functions for the predictors, which enables flexible modelling of complex, non-linear relationships (Schoch et al., 2018). These smooth functions are often represented through splines or other basis functions, while regularization techniques are employed to manage their smoothness and prevent overfitting (Everaert et al., 2017). The structure of GAM can be represented as:

$$g\left(E\left(Y\right)\right)= \beta_0 + f_1\left(x_1\right)+f_2\left(x_2\right)+\ldots+f_n\left(x_n\right)+\epsilon \tag{1}$$

The model connects one response variable, Y, with several predictor variables, X_i. The $f_i\left(x_i\right)$ denotes the smooth function for the i^{th} predictor. In the GAM Model, the Akaike Information Criterion (AIC) is used to evaluate and compare the model's fit to the data, balancing goodness-of-fit with model complexity. The model with the lowest AIC is often chosen because it provides the best balance of model fit and complexity (Chesnaye et al., 2025; Pratiwi et al., 2025). The AIC is described as:

$$\mathrm{AIC}=-2\,\mathrm{In}\ \left(\mathrm{L}\right)+2\mathrm{p} \tag{2}$$

where L is the likelihood function and p is the number of parameters. In the present study, a total of 36 sampling data recorded from 2021 to 2023 were used for the model. 6 different water quality parameters, viz. water temperature, specific conductivity, rainfall, atmospheric temperature, Free CO_2, and pH, were considered as predictors, with female GSI value as the response variable. Here, predictors were added step by step to see their contributions, which improved the model's predictive power. R software was used to apply the GAM model with an identity link function. The model is explained as: Gam (GSI) = s(WT) + s(COND) + s(RF) + s(AT) + s(FCO2) + s(PH), where WT: Water temperature, COND: Specific Conductivity, RF: Rainfall, AT: Atmospheric temperature, FCO_2: Free CO_2, pH: pH. Also, s (.) is the spline smoothing function of the variables.

3 Results

3.1 Ecological parameters

The water quality parameters of the studied site of river Ganga are depicted in Table 1. The water temperature of the river water ranged from 18.1 to 33.9 °C. The pH of the river water ranged from 7.5 to 8.6, suggesting that the river water is somewhat neutral to slightly alkaline in nature. The dissolved oxygen concentration varied from 4.5 to 8.8 mg L^{-1}, sustaining within the optimal range for fish. The mean value of total hardness (135 ± 13.69) and total alkalinity (155.06 ± 16.32) were found to be within the optimum range. The salinity value (0.04 ± 0.02) was observed to be negligible indicating an oligohaline water. The electrical conductivity measured 244 µScm^{-1}, and the water transparency was within the standard range of 11.2 to 110 cm in the river. The total dissolved solids (TDS) were measured between 220 and 375 mg L^{-1}. Nutrient characteristics such as total phosphate fluctuated between 0.012 and 0.44 mg L^{-1}, whereas nitrate (NO_3^-) ranged from 0.004 to 0.29 mg L^{-1}.

3.2 Gonado-somatic index (GSI)

Tables 2 and 3 provide an overview of the relationship between length classes and reproductive parameters of Hilsa fish, with a particular focus on the Gonadosomatic Index (GSI), which serves as an indicator of reproductive condition. For females, variations in the GSI

Table 1 Water quality parameters (Mean ± SD) at the Farakka site of river Ganga in West Bengal

Water quality parameters	Result (Mean ± SD)
Water temperature (°C)	28.85 ± 4.42
Dissolved Oxygen (mg L^{-1})	7.31 ± 1.46
Free Carbon dioxide (mg L^{-1})	6.2 ± 3.7
pH	8.03 ± 0.36
TDS (mg L^{-1})	224 ± 6.53
Electrical conductivity (µS cm^{-1})	244 ± 6.65
Total Hardness (mg L^{-1})	135 ± 13.69
Total Alkalinity (mg L^{-1})	155.06 ± 16.32
Salinity (ppt)	0.04 ± 0.02
Transparency (cm)	45.10 ± 39.02
Nitrate (mg L^{-1})	0.03 ± 0.04
Total Phosphate (mg L^{-1})	0.196 ± 0.11

Table 2 Gonado-Somatic index (GSI) of female *Tenualosa Ilisha* at different size range

Length cla	Mean total length mm ± SD	Mean body weight g ± SD	Mean gonad weight g ± SD	Mean GSI % ± SD
145–174	166 ± 7.84	48.3 ± 9.19	3.88 ± 1.74	7.91 ± 2.87
175–204	191 ± 7.72	79.5 ± 11.4	6.63 ± 2.31	8.12 ± 1.09
205–234	219 ± 7.91	108.3 ± 12.4	10.32 ± 4.10	9.32 ± 4.5
235–264	245 ± 5.7	155.6 ± 17.62	12.50 ± 5.0	8.21 ± 3.4
265–294	273 ± 4.04	210.6 ± 14.97	19.22 ± 7.50	9.43 ± 4.23
295–324	307 ± 5.06	268 ± 13.94	17.93 ± 8.09	6.63 ± 4.11
325–354	341 ± 10.06	603 ± 33.24	22.98 ± 6.97	3.81 ± 2.11

Table 3 Gonado-Somatic index (GSI) of male *Tenualosa Ilisha* at different size range

Length class (mm)	Mean total length mm ± SD	Mean body weight g ± SD	Mean gonad weight g ± SD	Mean GSI % ± SD
60–99	70.5 ± 14.8	31.5 ± 4.90	-	-
100–139	125.7 ± 10.57	23.2 ± 9.12	0.20 ± 0.02	0.15 ± 0.03
140–179	165.1 ± 9.80	43.5 ± 11.96	0.38 ± 0.03	0.89 ± 0.12
180–219	199.5 ± 11.42	78.4 ± 15.92	0.86 ± 0.06	0.95 ± 0.07
220–259	231.6 ± 10.08	116.9 ± 22.70	1.87 ± 0.08	0.88 ± 0.09
260–299	272.9 ± 9.7	202 ± 41.80	2.59 ± 1.29	1.24 ± 0.74
300–339	308.5 ± 11.9	216.2 ± 16.90	3.06 ± 0.88	1.40 ± 0.31
340–379	363.2 ± 9.24	480.6 ± 7.30	3.10 ± 0.89	1.87 ± 0.50

were recorded at various length groups ranging from 4 to 13.82 during the entire study period (Fig. 2). Normal growth and reproductive development is indicated by the steady increase in mean body weight and gonad weight as the length class increases from 145 to 174 mm to 325–354 mm. In the present study, the GSI values exhibited a non-linear trend. The GSI values initially increased with length, rising from 7.91% in the smallest length class to a maximum of 9.43% in the 265–294 mm. This indicates that mid-sized Hilsa are at or approaching optimal reproductive status. Interestingly, the GSI values do not follow a strictly linear trend. Initially, the GSI increases with size, rising from 7.91% in the length class 145–174 to 9.43% in the 265–294 mm class, suggesting that mid-sized Hilsa are at or near peak reproductive condition. However, the GSI drops significantly beyond this length, groups declining to 6.63% and 3.81% respectively. The elevated values of GSI occurred during the onset of winter (November to December) in the river, which was found to decrease gradually, suggesting that Hilsa breed either within November or in the early days of December (Fig. 3.). This drop in GSI may also suggest that larger individuals have either completed their spawning phase or are approaching a resting stage in their reproduc-

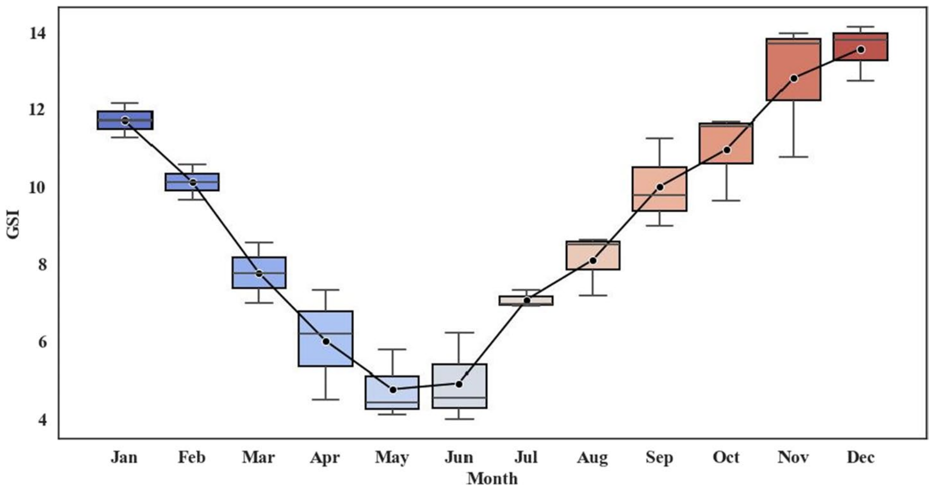

Fig. 2 Monthly variation in GSI indicating breeding pattern of *Tenualosa ilisha* (female) in Farakka, West Bengal (from 2021 to 2023)

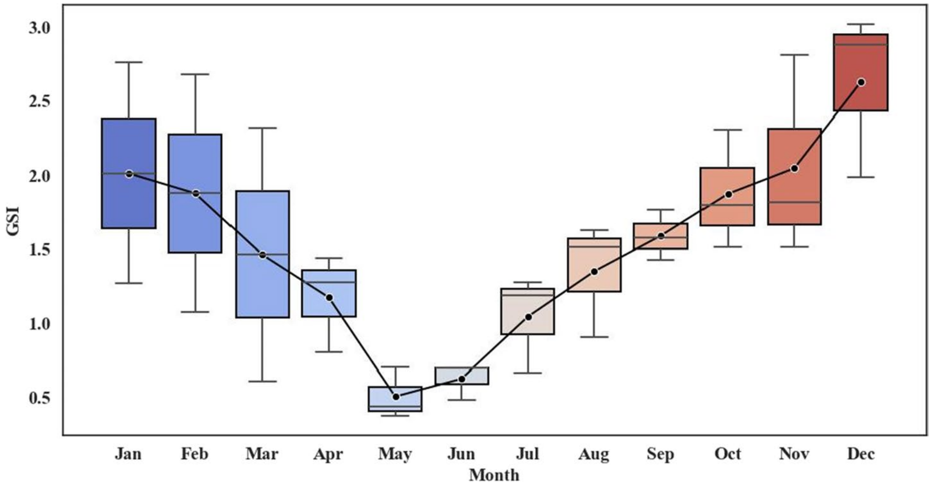

Fig. 3 Monthly variation in GSI indicating breeding pattern of *Tenualosa ilisha* (male) in Farakka, West Bengal (from 2021 to 2023)

tive cycle. The data indicate that the reproductive activity of Hilsa increases in the mid-length classes and declines in both the smallest and largest length groups. In the case of male specimens, the highest GSI (1.87 ± 0.50) was recorded in the length range of 340–379 mm, while the lowest was observed in the length class of 100–139 mm (0.15 ± 0.03). These results suggest that =male hilsa exhibit greater gonadal development with an increase in size, reflecting increased reproductive maturity with growth. Similarly, the male specimens showed peak GSI values during winter (November to December).

3.3 Fecundity

Fecundity is a vital measurement in fish conservation biology, as it offers valuable insights into estimating the abundance and reproductive capacity of a specific population (Ghosh et al., 2023; Rayhan et al., 2023). From the present study, the mean ova of *T.ilisha* ranged between 1,02,110 and 2,66,800 (Table 4) in the mean length range of 145–354 mm and 48.30–603 g of body weight (Fig. 5).

Table 4 Detail length-wise fecundity of female *Tenualosa Ilisha*

Length class (mm)	Mean total length mm ± SD	Mean body weight g ± SD	Mean gonad weight g ± SD	Mean fecundity (thousand) ± SD
145–174	166 ± 7.84	48.3 ± 9.19	3.88 ± 1.74	102.1 ± 12.87
175–204	191 ± 7.72	79.5 ± 11.4	6.63 ± 2.31	118.3 ± 17.23
205–234	219 ± 7.91	108.3 ± 12.4	10.32 ± 4.10	122.7 ± 16.34
235–264	245 ± 5.7	155.6 ± 17.62	12.50 ± 5.0	107.9 ± 15.27
265–294	273 ± 4.04	210.6 ± 14.97	19.22 ± 7.50	182.7 ± 10.28
295–324	307 ± 5.06	268 ± 13.94	17.93 ± 8.09	216.6 ± 14.05
325–354	341 ± 10.06	603 ± 33.24	22.98 ± 6.97	266.8 ± 24.11

3.4 3.4. Size at maturity

In the present findings, the female and male *T. ilisha* attained the length at first maturity (L_m) at 50% was 252 mm and 165 mm, respectively (Figs. 4a-b). The sexual maturity of *T. ilisha* in the Farakka region of the River Ganga is complex, as 25% of the female specimens were found to mature below 200 mm, indicating an early maturation (Fig. 4a).

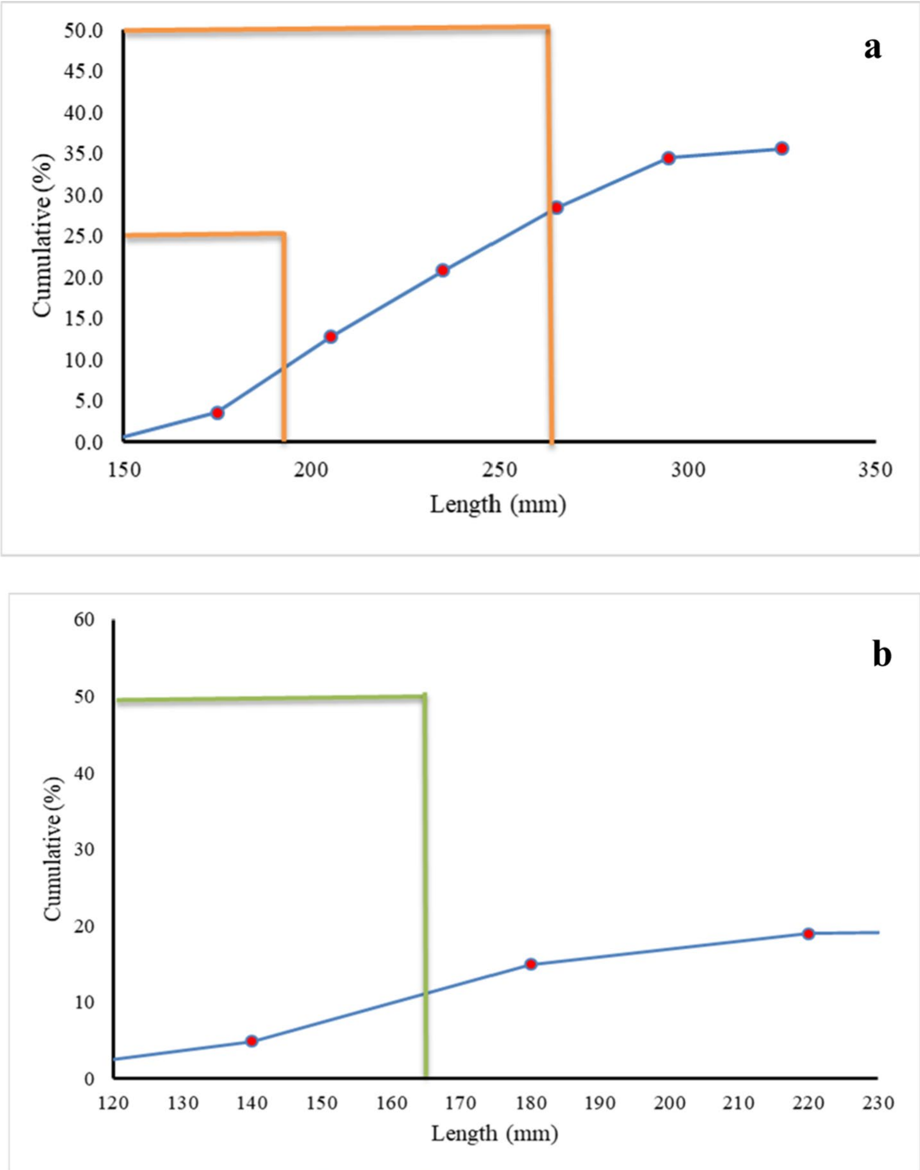

Fig. 4 (**a-b**). Length at first maturity (L_m) for female and male *T.ilisha*

3.5 Regional climate change pattern

The climatic trend was analyzed for the studied region from 1985 to 2023 and is displayed in Fig. 5(a-b). The average atmospheric temperature indicated an increasing trend ($R^2=0.293$) with a rapid increase of 0.98 °C over the last five years for the long period average (LPA) from 1985 to 2023. However, overall rainfall over the same period showed a declining trend ($R^2=0.27$), with a drop of 380.10 mm over the previous five years when considering the LPA.

3.6 Climato-hydrological influence and GSI

TheKarl-Pearson correlation was used to determine the relationship between rainfall (RF), atmospheric temperature (AT), and the Gonadosomatic Index (GSI) for female fish with three different seasons (premonsoon, monsoon and post monsoon) separately (Table 5).

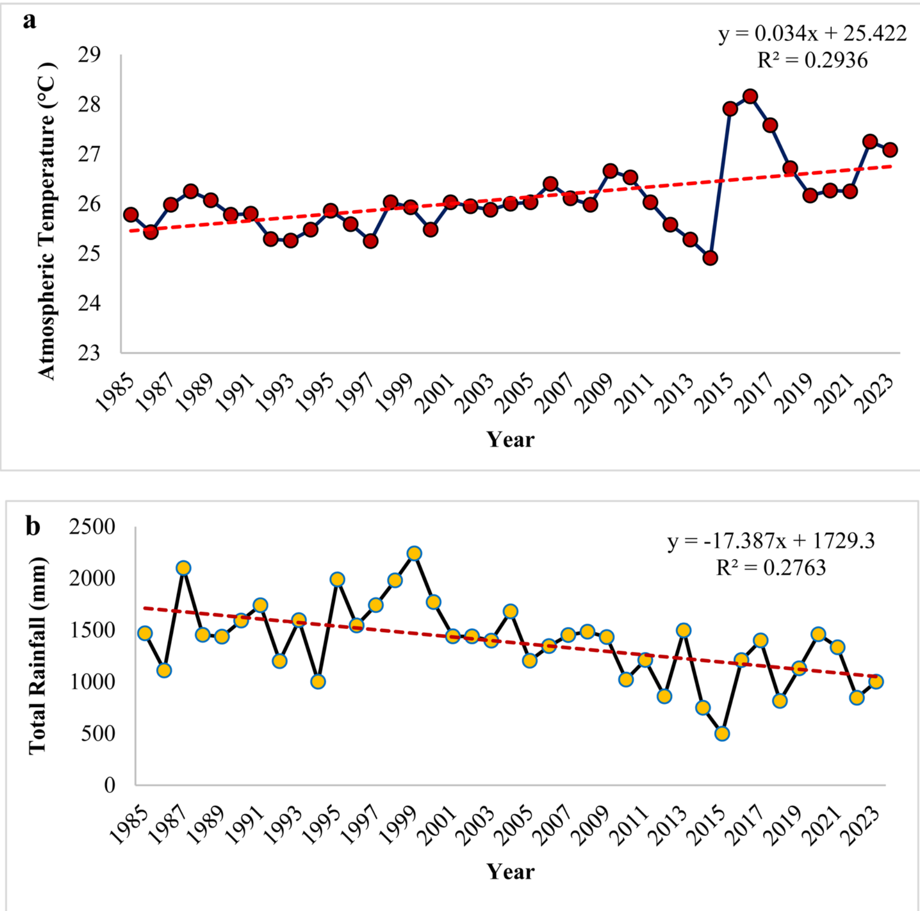

Fig. 5 Decadal change analysis in atmospheric temperature (**a**) and total rainfall (**b**) trend in the studied region from 1985 to 2023

Table 5 Karl-Pearson correlation coefficient between RF vs. GSI(F) and AT vs. GSI(F)

Seasons	RF vs. GSI(F)		AT vs. GSI(F)	
	r	*p*-value	*r*	*p*-value
Pre-Monsoon	0.41*	0.032	0.45*	0.027
Monsoon	0.49*	0.011	−0.72*	0.001
Post-Monsoon	−0.06	0.088	−0.69*	0.026

*Significant at 0.05 level; *r*: correlation coefficient. *RF* Rainfall; *AT* Atmospheric temperature; *GSI(F)*: Gonadosomatic Index for female

During the pre-monsoon season, both RF and AT significantly positively correlate with GSI ($r=0.41$ and $r=0.45$, respectively), indicating that higher rainfall and temperature may be linked with increased breeding activity. In the monsoon season, RF has a significantly positive correlation ($r=0.49$) with GSI. At the same time, AT shows a significantly negative correlation ($r=-0.72$), suggesting that rainfall and temperature support reproductive development in the pre-monsoon season. In the post-monsoon season, RF shows a slightly negative correlation with GSI ($r=-0.06$), while AT has a strong negative correlation (−0.69), indicating that higher temperatures may reduce reproductive activity significantly. These seasonal patterns highlight the varying influence of rainfall and temperature on female reproductive cycles.

3.7 Generalized additive model (GAM)

A Generalized Additive Model (GAM) was employed to determine the impact of water quality and environmental parameters on female GSI values. It describes the non-parametric and semi-parametric regression investigation for revealing relationships between response and predictor variables. In this analysis, a total of 36 sampling data recorded from 2021 to 2023 were used for the model. 6 different water quality parameters, viz. water temperature, conductivity, rainfall, atmospheric temperature, Free CO_2, and pH, were considered as predictors, with female GSI as the response variable. Here, predictors were added step by step to see their contributions, which improved the model's predictive power. R was used to apply the GAM model with an identity link function and a Gaussian distribution. The model is explained as -.

Gam (GSI) = s(WT) + s(COND) + s(RF) + s(AT) + s(FCO2) + s(PH); where s(.) is the spline smoothing function of the variables. Where: AT = Atmospheric temperature, COND = Conductivity, RF = Rainfall, PO_4^{3-}=Phosphate, SAL = salinity, FCO_2 = Free CO_2, TRA = Transparency, WT = Water temperature, ALK = Alkalinity, HARD = Hardness, NO_3^{-}= Nitrate, TDS = Total Dissolved Solids).

The stepwise GAM model was used in this study to examine the predictors affected the response variable. Analysis showed that the model predictive power progressively improved with the incremental inclusion of predictors. Using all six predictor variables (water temp. + conductivity + rainfall + atmospheric temp.+ Free CO_2 + pH), the final model (Mod6) had the lowest Akaike Information Criterion (AIC) score of 81.86 and explained 94.3% of the variances (Table 6).

Each water quality parameter has an influence on the GSI value. Initially, it was applied to each parameter to assess their influences on GSI value. The most important factor influencing the female GSI value was found to be water temperature (57.1% deviance explained), which was followed by conductivity, rainfall (mm), air temperature, free CO_2 and pH. Each predictor parameters influence curve on the GSI value as determined by GAM is shown in Fig. 6.

Table 6 The influence of each predictor variable on the GSI value derived from the GAM model

Model	Predictor	Deviance explained (%)	AIC
Mod_0	C (Null model)		170.27
Mod_1	c + s(WT)	57.1	159.52
Mod_2	c + s(WT) + s(COND)	63	143.63
Mod_3	c + s(WT) + s(COND) + s(RF)	80.3	125.72
Mod_4	c + s(WT) + s(COND) + s(RF) + s(AT)	92.4	115.20
Mod_5	c + s(WT) + s(COND) + s(RF) + s(AT) + s(FCO2)	94.3	111.73
Mod_6	c + s(WT) + s(COND) + s(RF) + s(AT) + s(FCO2) + s(PH)	94.3	81.86

WT Water temperature; *AT* Atmospheric temperature; *COND* Conductivity; *RF* Rainfall; FCO_2 Free Carbon dioxide; *PH* pH

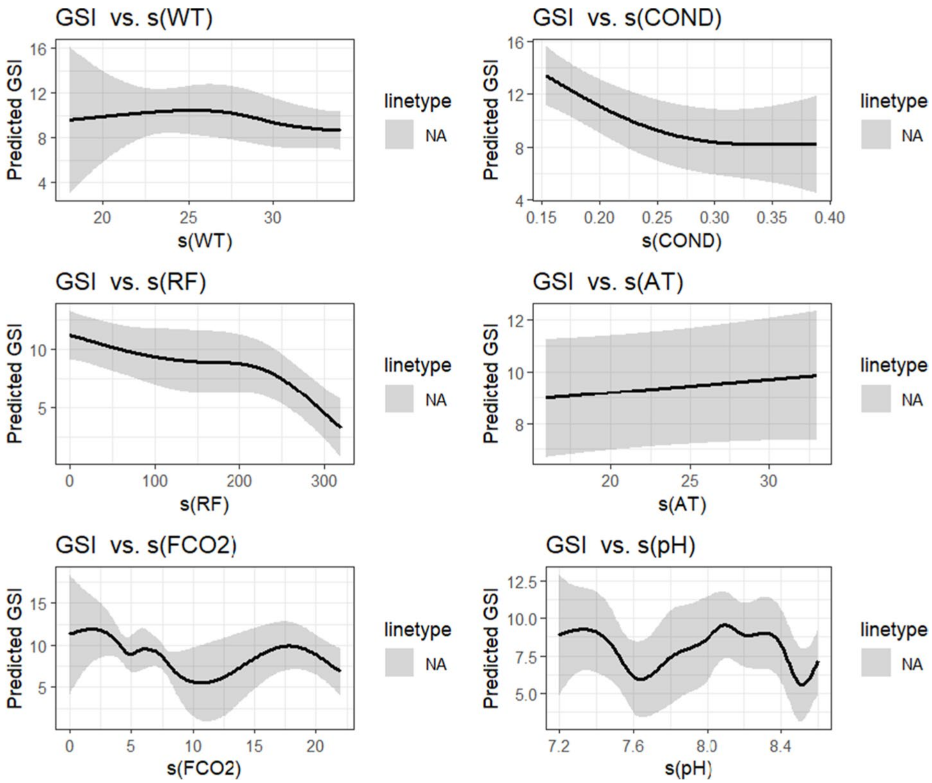

Fig. 6 Generalized additive model (GAM) for GSI concerning water quality and environmental parameters. Note: WT = water temperature, COND = Conductivity, RF = Rainfall, AT = Atmospheric temperature, FCO_2 = Free carbon dioxide, pH = pH

The ecological parameters, along with environmental factors such as atmospheric temperature and water temperature, exhibited linear effects on GSI values, while conductivity, rainfall, Free CO_2, and pH demonstrated non-linear patterns in the response curve. Narrow confidence intervals indicated high reliability in the results, whereas wider intervals suggested less consistency in predictions Higher ranges of conductivity and rainfall were shown to be associated with a consistent decrease in GSI values. In contrast, atmospheric temperature showed a positive trend, with increasing GSI values. The water temperature had a slightly non-linear trend; but, positive impact on GSI values within the range of 25 to 28 °C. Additionally, water pH demonstrated a more non-linear but favourable impact on GSI values.

The GAM model demonstrated strong predictive performance with an AIC of 81.863, indicating a good balance between fit and complexity. The MSE of 0.154, RMSE of 0.392, and MAE of 0.283 reflect low prediction errors, confirming its accuracy. The MAPE of 3.48% shows minimal average deviation from actual values, while the R-squared value of 0.98 indicates that the model explains 98% of the variance. These metrics collectively highlight the model's high reliability and accuracy.

4 Discussion

The Hilsa (*Tenualosa ilisha*) fishery in River Ganga holds profound ecological, cultural, and economic significance in the Indian subcontinent, serving as a cornerstone of livelihood for millions of riparian and estuarine communities. The River Ganga itself functions as a critical ecological corridor, supporting a diverse array of biota including benthic invertebrates, plankton communities, and a variety of freshwater fish species (Sahoo, 2015). Factors like water temperature plays an important function in numerous natural processes in the aquatic environment which can influence fish metabolism and reproductive cycles (Mugwanya et al., 2022). A change in the temperature may trigger a change in different parameters. The minimum average water temperature in the Farakka region was 28.85 °C, in sharp contrast to the colder segment of the river at 12.9 °C, as documented by Vass et al. (2009), suggesting distinct ecological regimes along the river's course. Recently, Tiwari et al., 2022 observed that the dissolved oxygen values were greater than 6.23 mg L^{-1} from the present study site which were in close conformity with the present findings. Elevated CO_2 levels can lower pH, leading to acidification, which may harm fish gills and overall health having significant impact on the metabolic process (Palit et al., 2018). Several authors have documented the pH of river Ganga to be alkaline (Mukherjee et al., 1993; Haritash et al., 2016; Tiwari et al., 2022). In the present study, the mean pH value of 8.21 was recorded in the Farakka region, which coincides with our present study. Total Dissolved Solids (TDS) quantifies inorganic salts, organic matter, and other dissolved substances in water (Weber-Scannell & Duffy, 2007). The present value of TDS was much below the permissible limit as per BIS standard (500 mg L^{-1}). The average electrical conductivity of the water was 244 ± 6.65 µS cm^{-1} which was also well below the acceptable range of 20 to 500 µS cm^{-1} (Chatterjee et al., 2025). In the present study, the value of total hardness (135 ± 13.69 mg L^{-1}) in the Farakka region. Similar results were also reported by Tiwari et al., 2022 from the region. The determination of total alkalinity helps in understanding the buffering capacity of the river (Hare et al., 2020). The present alkalinity value was slightly higher than the reported value of 124. 7 mg L^{-1} from the region (Tiwari et al., 2022). The salinity indicated a negligible value in the region which confirms that the salinity of freshwater found in lakes, ponds, and rivers is 0.5 ppt or below (Shaha et al., 2022). Transparency Determines the amount of light penetrates into the water column suggesting less turbidity and visual indicator of the river.

The present findings of transparency were in line with the findings of Tiwary et al., 2022. Similarly, the water nitrate and phosphate level were also determined to be within the range that was most conducive to plankton growth (Qotbi et al., 1996; Ahsan et al., 2012).

The GSI is a commonly assessed ratio of gonad weight to body weight, facilitating the comparison of reproductive status among different fishes (Zeyl et al., 2014; Mian et al., 2017). Recent studies focusing on the breeding and spawning season of Hilsa, particularly in the freshwater section of the river Ganga, is scarce. The occurrence of two peak breeding seasons of Hilsa was reported by several workers in the rivers of India and Bangladesh (Pillay, 1958; Quddus et al., 1984). Pillay, 1958 in a report had concluded the peak breeding spawning season of Hilsa occurs from the occurrence of the south-west monsoon to November and then in winter extending from January to March. Similar results of monsoon breeding of Hilsa in the freshwater section of River Ganga were also demonstrated by Nair (1958) and Chandra (1962). Bhaumik et al., 2012a highlighted that the peak breeding period of the species extended from January to March. The Gonadosomatic Index (GSI) of both male and female *T. ilisha* peaked between October and December, followed by a gradual decline from January onwards. This observed peak differs from earlier reports suggesting a bimodal spawning pattern during the monsoon and winter seasons from River Ganga (Pillay, 1958; Nair, 1958; Chandra, 1962; Ghosh & Nangpal, 1970). Ghosh and Nangpal (1970) stated that the winter breeding of Hilsa in the lower Ganga around Bhagalpur (above Farakka) occurs from late February or early March to the last week of April. Nair (1958) stated that the oogenesis in Hilsa peaked in March in River Hooghly, and subsequently, the ova undergo resorption. In a lower estuarine stretch of river Ganga, the Hilsa breeding commences in July and extends till November, which is said to be extended till February until the winter recedes in other sites (Ghosh and Nangpal, 1970). Notably, our findings suggest a possible shift in the breeding periodicity, potentially influenced by site-specific environmental factors such as water temperature, flow alteration, and turbidity. In terms of sexual maturity, 50% of the females attained first maturity (L_m) at 252 mm, and males at 165 mm, which is substantially lower than previous records from the River Ganga (Mathur, 1964; Shafi & Quddus, 1974). The sexual maturity of *T. ilisha* in the Farakka region of River Ganga is complex as significant proportion (25%) of females in the Farakka stretch matured below 200 mm, indicating a trend towards early maturation. This precocious development may reflect stress-induced reproductive plasticity under environmental and anthropogenic pressures, such as altered flow regimes, thermal pollution from nearby power plants, and intense fishing activity (Ahammad et al., 2021; Bhaumik et al., 2012b). Similar trends of early maturation have been reported in Hilsa populations from Chilika lagoon and the Meghna estuary (Ramakrishnaiah, 1972; Islam et al., 2016). These variations across geographical locations emphasize the influence of local climatic, the lunar cycle, hydrological, and ecological factors on the reproductive biology of Hilsa, suggesting a complex and adaptive spawning response to habitat fragmentation and environmental perturbations within the Gangetic basin.

The Minimum Legal Size (MLS) for Hilsa (*Tenualosa ilisha*) is generally determined based on the mean length at first maturity (L_m), often using the 50% maturity threshold to ensure sustainable harvest practices (Rayhan et al., 2023). In India, the L_m for *T. ilisha* has been estimated at approximately 207–208 mm (Bhaumik et al., 2012a), yet regulatory policies have set a slightly higher prohibiting the capture of Hilsa below 230 mm total length in estuarine and bay mouth regions during the critical breeding season from February to April, as per the West Bengal Gazette Notification (2013) (Sajina et al., 2020). In contrast, studies from Bangladesh have reported considerable sexual dimorphism in maturity lengths, with males maturing at 210 mm and females at 320 mm (Shafi et al., 1978), highlighting significant regional and sex-based variability. This variation underscores the complex interplay between genetics, environmental conditions, and fishing pressure, all of which influence maturation thresholds. The disparity in MLS across different areas reflect the absence of integrated geographical-specific regulatory frameworks, despite the migratory and trans-boundary behaviour of Hilsa. The current findings of early maturation in some populations particularly females maturing below 200 mm raise critical concerns regarding the biological effectiveness of existing size regulations. Premature harvesting of individuals not only reduces spawning potential but may also induce long-term evolutionary consequences, such as truncated growth and earlier maturation under selective fishing pressure (Jørgensen et al., 2007). Therefore, MLS must be revised based on current biological assessments and location specific maturity data, instead upon the threshold limits. Furthermore, enforcement of appropriate gear restrictions especially the regulation of gill net mesh sizes is vital to avoid recruitment overfishing and ensure the conservation of this economically and culturally significant species.

The minimum and maximum fecundity values recorded in the present study were significantly lower than those reported in earlier studies from the Hooghly estuary and upper stretches of the River Ganga. For instance, the fecundity estimates observed by Pillay (1958) and De (1986) from the lower Ganga (Hooghly estuary), as well as those reported by Mathur (1964) and Swarup (1958) from the Allahabad (Prayagraj) and Varanasi regions, respectively, exceeded the present findings. Bhaumik et al. (2012b) documented a broad fecundity range for *T. ilisha* from 44,002 to 1,554,894 eggs in specimens measuring 208–475 mm in length and weighing 105–1175.5 g from the Hooghly-Bhagirathi system. In contrast, the current study from the Farakka stretch revealed a more irregular pattern, with mean fecundity initially increasing with body weight up to the 205–234 mm length class, followed by a decline and a subsequent rise in the 265–294 mm range. This non-linear trend suggests possible intra-population variability, likely influenced by physiological stress, environmental factors, or suboptimal habitat conditions (Bagenal, 1978; Canosa & Bertucci, 2023). Saifullah et al. (2004) emphasized body weight as the most reliable predictor of fecundity in Hilsa; however, the inconsistencies observed in this study point toward more complex biological interactions, including variations in feeding success, energy allocation, and spatial competition among individuals (Mookerjee & Mazumdar, 1946; Bagenal, 1957; Mohamad et al., 2024; Rayhan et al., 2023). Additionally, factors such as age, gonadal development, and genetic makeup can influence fecundity even within the same size class (Mohamad et al., 2024). The observed reduction in fecundity may also reflect broader environmental stressors, including altered flow regimes, pollution, and climate-related alterations such as changes in temperature and precipitation, all of which are known to disrupt reproductive cycles in tropical fish (Owiti & Dadzie, 1989; Brulé et al., 2022). Collectively, these findings highlight the sensitivity of reproductive output to both internal physiological and external ecological drivers, underscoring the need for localized reproductive assessments in formulating effective conservation and management strategies for Hilsa populations in different stretches of the Ganga.

In the present study, distinct seasonal variations in temperature were observed, with the lowest temperatures recorded during December and January, and peak temperatures occurring between April and June. These temperature patterns are consistent with broader climatic observations across India. Dash et al. (2009) reported a weakening of the summer monsoon circulation, correlating with irregular rainfall distribution. Guhathakurta and Rajeevan (2008) further noted that key monsoon months like June, July, and September have contributed less to the total annual rainfall in several Indian subregions in recent decades. Studies by Rathore et al. (2013), Gaur et al. (2021), and Das Ghosh et al. (2023) have also documented similar changes, revealing long-term deviations in temperature trends. Climate variability, especially rising temperatures and altered precipitation patterns, has been shown to significantly influence the eco-hydrology of aquatic ecosystems (Ehteram et al., 2018). Moreover, long-term spatial and temporal analyses by Radhakrishnan et al. (2017) and Mondal et al. (2015) identified a positive trend in temperature and a concurrent declining trend in rainfall across various parts of India. These shifting climatic patterns have potential implications for riverine environments, affecting temperature regimes, water availability, and ultimately, the biological responses of aquatic organisms.

The highest Gonadosomatic Index (GSI) values for *T. ilisha* in the River Ganga were recorded during the post-monsoon period, specifically between November and January. These findings are partially aligned with earlier reports by De (1980, 1986), who observed an extended spawning season for *T. ilisha* ranging from September to March. Environmental and climatic variables particularly temperature and rainfall are known to be critical determinants of reproductive timing, distribution, and abundance in freshwater fishes (Borah et al., 2023). Numerous studies have demonstrated how seasonal and climatic fluctuations influence species diversity, abundance, and breeding phenology (Visser & Both, 2005; Brodman, 2009; Debnath et al., 2024). Additionally, the broader impacts of climate change on freshwater fish populations, including shifts in reproductive behaviour and habitat suitability, have been well documented (Sarkar et al., 2012; Beatty et al., 2014; Whitney et al., 2016; Kim et al., 2020; Carosi et al., 2021).

In the current study, a positive correlation was observed between mean air temperature and GSI in female *T. ilisha* during the pre-monsoon season, highlighting the influence of temperature on reproductive physiology. Previous research supports this trend, confirming that temperature significantly influences reproductive cycles (Svedaung et al., 1996; Lukšiene & Svedäng, 1997; Adger et al., 2005) and growth rates in fish (Brander, 1995). Sharma et al. (2014) further reported that water temperatures ranging from 29 to 32 °C is optimal for the spawning of *T. ilisha*, also noting a strong influence of temperature on GSI in Indian major carps. These observations collectively underscore the pivotal role of thermal regimes in regulating reproductive success in *T. ilisha*, particularly under the increasing unpredictability of climate-driven environmental changes.

A steady decline in GSI values (mean 4.11) was observed in association with reduced annual rainfall, suggesting a possible link between climatic variability and reproductive performance in the species. Earlier researchers have reported similar observations, who found that altered rainfall patterns along with changes in river water turbidity and flow can adversely impact the spawning success of freshwater fish species (Vass et al., 2009; Khatun et al., 2019). *T. ilisha* is known to prefer low-salinity freshwater zones for spawning during its monsoon migration. Pati and Pati (1982) demonstrated a significant positive correlation between rainfall intensity and Hilsa catch, reinforcing the role of rainfall as a key environmental parameter in triggering upstream migration and reproduction. River discharge, rainfall, water temperature, and salinity are recognized as major drivers of Hilsa migration and breeding, all of which are increasingly influenced by climate change. These factors collectively contribute to shifts in the spatial and temporal dynamics of Hilsa migration patterns and reproductive success (Sahoo & Wahab, 2024a).

Ahammad et al. (2021) emphasized that early gonadal development in *T. ilisha* is primarily influenced by environmental fluctuations and genetic variation, both of which contribute significantly to irregular spawning periodicity. The findings of the present study indicate that temperature fluctuations are a fundamental driver of early gonadal maturation in *T. ilisha*. Previous research suggests that the Cyt b gene of mitochondrial DNA play a regulatory role in this early reproductive development. Miah (2015) also documented shifts in spawning patterns due to both climatic variability and anthropogenic pressures, advocating for adaptive management strategies to ensure sustainable exploitation of natural stocks. Mondal (2012) noted that rising water temperatures can act as a physiological trigger for the onset of reproductive processes in various fish species. In support of this, Sarkar et al. (2021) observed early maturation in *Gudusia chapra* (Family: Dorosomatidae) under the combined influence of climate change and overfishing. Similarly, studies by Nair and Namcollas (1958) and Kay et al. (2018) confirmed that increasing sea surface temperatures play a crucial role in accelerating gonadal development in Hilsa populations of the Bay of Bengal. The present study exhibited a similar conclusion, which is that early maturation of Hilsa is conceivable under current environmental stressors.

4.1 Guidelines to the sustainable hilsa fisheries of river Ganga

Given the possible challenges to Hilsa fisheries, the establishment of appropriate management standards and their effective implementation are essential. Besides undulating climatic effects, the baseline data on riverine ecology and fisheries must be defined to address current issues. The present investigation recommends several important components for the implementation of management interventions, specifically:

- *Restoration of Habitat*: Habitats are degrading due to pollution, siltation, and the alteration of riverine ecosystems due to unregulated industrial and agricultural activities. Urban waste discharge into the Ganga has degraded the Hilsa's breeding and feeding habitats.
- *Climate change mitigation*: Investigation on the potential for adapting Hilsa fisheries to climate-induced shifts in migratory patterns, such as changing the fishing seasons. Investment in climate-resilient infrastructure for aquaculture to sustain populations.
- *Regulation of juvenile and brooder overfishing*: Banning of small meshed gill nets and bag nets creating wanton destruction of Hilsa juveniles and brooders, especially during peak breeding and post-breeding months.
- *Management of Hilsa breeding grounds*: Prioritization of conservation of natural breeding grounds of Hilsa in River Ganga during peak breeding period.
- *Awareness and education among local fishers*: Creation of public awareness campaigns on the importance of Hilsa conservation for future generations involving the direct and indirect stakeholders.

5 Conclusion

The present findings on the reproductive biology of Hilsa in the freshwater stretch of the Farakka region in the Ganga River contribute critical insights into the life-history traits of this anadromous species, particularly under the growing influence of climate-induced environmental variability. Given that temperature fluctuations directly influence metabolic functions, reproduction, and food web dynamics, Hilsa populations remain highly sensitive to ongoing climate changes. Despite its national importance, research efforts on Hilsa within Indian river systems remain fragmented and limited in scope. This lack of focused ecological and physiological data has constrained the formulation of adaptive management strategies. It is, therefore, imperative to implement long-term, multidisciplinary research frameworks to monitor climatic parameters, hydrological changes, and biological responses of Hilsa across its migratory route. Such an integrated approach would not only help delineate climate-resilient management zones but also help in effective policymaking. Furthermore, securing the future of the Hilsa fishery necessitates the development of dynamic, climate-responsive conservation strategies. These must include the enforcement of minimum legal sizes (MLS), spawning sanctuaries, and temporal fishing bans aligned with reproductive cycles. Additionally, economic incentive schemes such as community-based alternative livelihoods and capacity-building programs can render conservation efforts and check poverty in fishing-dependent communities. Through integrated cross-sector collaboration and adaptive management approaches, the sustainable restoration of this iconic species can be achieved.

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Archisman Ray: writing-original draft, formal analysis, methodology.
Saurav Kumar Nandy: Sampling, data analysis and writing draft.
Hena Chakraborty: Data visualization and presentation.
Arghya Kunui: Sampling and data curation.
Naba Kumar Acharjya: Assistance in collection of samples.
Sanatan Paul: Assistance in statistical analysis of data.
Amiya Kumar Sahoo: Review the manuscript.
Santhana Kumar V: Review the manuscript.
Dharmendra Kumar Meena: Review the manuscript.

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Data availability Data may be available upon reasonable request to the corresponding author.

Declarations

Ethical standards All authors have read, understood, and have complied as applicable with the statements on "Ethical responsibilities of Authors" as found in the Instructions for Authors.

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