



# Reproductive environment of the decreasing Indian river shad in Asian inland waters: disentangling the climate change and indiscriminative fishing threats

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## Abstract

The regional climate has significantly warmed with erratically declining annual rainfall and intensified downpour within a narrower span of monsoon months, which led to an increased trophic state ( $\approx$ algae) in most inland waters. Freshwater clupeids vitally control the aquatic food chain by grazing on algae. Despite increasing food availability, IUCN Red List® revealed 16 freshwater clupeids with a decreasing population trend. We investigated one such species' reproductive dependencies, *Gudusia chapra* (Indian river shad), in the lower Gangetic drainage (India) under a mixed context of climate change and overfishing. Monthly rainfall ( $\geq 60$ – $100$  mm) and water temperature ( $\geq 31$ – $32$  °C) are key breeding cues for females. The regional climate seems inclined to fulfill these through the significant part of the breeding season, and indeed the species has maintained consistent breeding phenology over 20 years. Other breeding thresholds relevant to fishing include size at first maturity ( $\geq 6.8$  cm; reduced by  $\sim 25$ – $36\%$ ) and pre-spawning girth (Girth<sub>spawn50</sub>  $\geq 7$  cm; first record). Girth<sub>spawn50</sub> is a proxy of the minimum mesh size requirement of fishing nets to allow safe passage of “gravid” females ( $+ 22\%$  bulged abdomen) and breed. The operational fishing nets (3–10 cm mesh) probably have been indulged in indiscriminative fishing of gravid females for generations. Under a favorably changing climate and food availability, existing evidence suggests a fishery-induced evolution in regional females (to circumvent such mesh sizes) through earlier maturation/puberty at smaller sizes. It could be an early warning sign of population collapse (smaller females  $\rightarrow$  lessening fecundity  $\rightarrow$  fewer offspring). Overfishing seemed to be a bigger threat than climate change.

**Keywords** Breeding thresholds · Breeding phenology · Mesh size · Pre-spawning girth · *Gudusia chapra* · Freshwater clupeids

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## Introduction

Global climate change is known to impact inland aquatic ecosystems and life-history events such as breeding phenology of fishes, ultimately augmenting or deteriorating the existing natural population (Myers et al. 2017; Sarkar et al. 2019a, b). It has implications for both biodiversity (conservation) and fisheries (exploitation). With increasing research and societal attention in this regard (Jarić et al. 2020), recently, an open-access database was launched (<https://ficli.shinyapps.io/database/>). It summarizes the available literature on fishes' phenological responses to changing climate worldwide (Krabbenhoft et al. 2020), e.g., changing temperature, rainfall, and flow scenarios. In the lower Gangetic basin of the Indian subcontinent, our regional climate has the following: (a)  $+ 0.4$  °C rise in mean air temperature since the 1980s, (b) with

erratically declining annual rainfall (annual range < 1000 to 2000 mm; 135.6–257 mm decline in rainfall since 1980s), and (c) intensified downpour within a narrower span of monsoon months (May to August) (Sarkar et al. 2017; Karnatak et al. 2018; Naskar et al. 2018). Concomitantly, some inland waters are slowly progressing towards having more algae. Approximately 20% of the region's floodplain wetlands have gradually become eutrophic (Sarkar et al. 2020). Increasing air temperature and decreasing water depth were attributed to such transitions, besides anthropogenic factors like sewage and agriculture (Sarkar et al. 2020). Changing climate has been demonstrated to affect every stage of reproductive development in fishes, from puberty to spawning, through endocrine regulation changes along the brain-pituitary-gonad axis (Alix et al. 2020).

Clupeids include some of the world's most prized wild captured fishes like herrings, menhadens, sardines, shads, and sprats. Although most species are marine or anadromous, only a handful of them (70 out of 402 described species) are inhabiting freshwater (Mary et al. 2017). Clupeids are regionally presumed to be sensitive to changing climate with low reproductive resilience in adapting to climatic variabilities. A prologue of such presumptions can be found in Hossain et al. (2019), Sahoo et al. (2018), and Miah (2015). On a global scale, the ill effects of changing climate on marine clupeid reproduction and the ultimate manifestations on the herring stocks of the sea are somewhat documented (e.g., Ojaveer et al. 2015). However, existing studies on freshwater clupeids have been mostly traditional morphometrics and feeding-breeding biology oriented (e.g., Kumari et al. 2018, 2019, 2020; Ahamed et al. 2014; Hossain et al. 2010; Vinci et al. 2005). Assessments of the reproductive vulnerability of “freshwater clupeids” (in inland waters) to changing climate and other anthropogenic stressors have been scarce. A list of vulnerability assessments done worldwide on clupeids to climate change has been provided as a [supplementary appendix](#) (sorted from Krabbenhoft et al. 2020). About 13 studies were encountered, assessing demographic to phenological responses to climate change ([supplementary appendix](#)). Although most of these studies utilized historical databases, such time-series datasets that are too parameter- and species-specific are often lacking in developing regions like ours (Sarkar et al. 2019b; Naskar et al. 2018). A metadata search in the latest IUCN Red List® revealed 16 freshwater clupeid species with decreasing population trend in inland waters (*Tenualosa ilisha*, *Alosa aestivalis*, *Alosa killarnensis*, *Gudusia chapra*, *Tenualosa thibaudeaui*, *Clupeonella abrau*, *Alosa immaculata*, *Alosa alabamae*, *Alosa algeriensis*, *Tenualosa reevesii*, *Tenualosa toli*, *Clupeonella puglisi*, *Sardinella tawilis*, *Tenualosa macrura*, *Coilia nasus*, and *Thryssa rastrosa*) (IUCN 2020). The present study has relevance since such studies are lacking in inland waters, especially from developing countries.

The species studied in the present work, *Gudusia chapra* (Hamilton, 1822), commonly known as the Indian river shad, is a freshwater clupeid native to the rivers Ganges, Brahmaputra, and Mahanadi, and adjoining floodplain wetlands (Froese and Pauly 2019). The fish belonging to the small indigenous fishes (SIFs) exhibits potamodromous migration and pelagic shoaling behavior and inhabits a wide range of freshwater habitats (Kumari et al. 2018). Like most clupeids, Indian river shads are mostly algal feeders, i.e., primary consumers or phytoplanktophagus (Rahman et al. 2008; James 1988). *G. chapra* has been classified as Least Concern (LC) but “decreasing population” category (IUCN 2020). A warning note is attached to the species assessment sheet stating that the population of *G. chapra* is declining within the Ganges drainage in India and Nepal (Chaudhry 2010). Previously, the zoological survey of India (ZSI) has also attached such a note in its record (Mishra et al. 2003). In India and Bangladesh, it is one of the most commercially important SIFs (small indigenous species), fetching fair market prices and supporting rural fisherfolk's livelihood (Mishra et al. 2003). *G. chapra* fetches at least 30% higher price in local Indian markets, in comparison to other SIFs such as *Amblypharyngodon mola* and *Puntius sophore* because of superior taste (authors' observations). They also present an excellent deal for the more impoverished population as a nutrient-dense food and provide nutritional security for the rural communities (Castine et al. 2017; Bogard et al. 2015). For example, *G. chapra* offers a nutrient profile of 15.2 g protein, 5.4 g lipid, and 1.6 g minerals (rich in Ca, K, and Mg) per 100 g of whole-body consumption (equivalent to ~ 7–8 fishes of ~ 10.6 cm length) (Mohanty et al. 2011).

Sporadic reports on the gradual disappearance of *G. chapra* from regional inland tropical waters exist (Chaudhry 2010; Vinci et al. 2005; Ghosh et al. 2018; Mondal et al. 2019; Mishra et al. 2003). During 1960–1970, Indian river shads were abundant in most inland waters (Rahman and Haque 2006; Mondal et al. 2019). What led to such a decline needs to be answered for the future security of this species. So far, successful domestication (captive seed production and rearing) of this species is non-existent—making in situ conservation the only available contingency. Therefore, a reproductive dependency assessment of *G. chapra* to changing climate was carried out. To understand the anthropogenic stress on the reproductive environment of *G. chapra*, indiscriminate fishing was also investigated. It was done by reviewing mesh size ranges of fishing gears used in their habitats. Such an effort is expected to contribute to prudent conservation planning. The existing regional presumptions on the climate-sensitive nature of reproduction in clupeids were validated for the first time. The following aspects were systematically analyzed to arrive at the results and recommendations: (a) quantification of biological thresholds for breeding (gonadosomatic index, pre-spawning fitness, sizes at maturity, and a novel parameter

parameterized as pre-spawning girth); (b) identification and quantification of key environmental cues for successful breeding (climatic and habitat parameters); (c) track shifts (if any) in present breeding phenology relative to historical records; (d) collate regional patterns of temperature and rainfall variability with observed reproductive traits; (e) derive minimum mesh size recommendations (from pre-spawning girth estimates) to ensure successful spawning of gravid females without being captured and collate with mesh sizes of operational fishing nets in the area.

## Materials and methods

### Study area and species selected for study

Five regional floodplain wetlands (average water spread area of 20–48 ha; depth range of 0.7–3 m) in lower Gangetic plains of West Bengal, India, were identified based on the available information regarding the presence of residential stocks of the target species: Chandania (22.57523° N, 88.43167° E), Mathura (22.55561° N, 88.28374° E), Bishnupur (24.65897° N, 88.155411° E), Katiganga (24.12507° N, 88.165088° E), and Chaltia (24.07205° N, 88.262249° E). We have employed local fishers to collect fish samples every month. All these wetlands share a common annual photo-thermal and precipitation regime (daytime temperature 17–36 °C; day length 11.7–12.2 h; monthly rainfall 0–500 mm). Additional information on the studied species, including a map of the study area (Fig. S1a) and the studied species (Fig. S1b), is provided in the supplementary material.

### Sample collection, measurements, and coding

In this study, 354 specimens (214 female, 140 male, and non-sexed) were collected using gill nets (mesh sizes 20 to 80 mm). Two consecutive breeding timing loops (end → start → end → start → end), hereinafter referred to as breeding cycles, were included in the sampling program between October 2017 and October 2019. Only females were selected as model sex owing to the ease in observing ovaries (compared to the testes) and easily demarcated gonadal maturity status. Also, the abdominal distension in gravid females is prominent, unlike mature males, which have somewhat slender abdomen (authors' observation); thus, making females more relevant for girth measurements to elucidate fishing threats. The fresh body weight (in g) and total length (cm) were taken. Maximum body depth (cm) was measured in each fish, i.e., the height of the widest part of the spindle-shaped body. The body depth was multiplied by 2 to give maximum body girth, hereinafter referred to as "girth." The girth is supposed to correspond to the complete circumference of a mesh (i.e., mesh size of a fishing net) if it wraps tightly around the

broadest part of the fish body (i.e., the point where the fish is trapped and cannot escape further).

Five maturity stages were considered in the present study: immature, maturing, mature, ripe, and spent. Females with "mature" and "ripe" stage ovaries were coded as "1," while the ones with immature, maturing, and spent ovaries were coded "0" (see supplementary material). In such instances, where the gonads were inconspicuous, the samples were not counted to avoid statistical errors. Fresh ovaries were also weighed (g) and preserved in 70% ethanol. In some specific months where only a few "recognizable" females/ovaries (post-dissection) were encountered in a breeding cycle, the data were pooled under a common month irrespective of the breeding cycle (e.g., January, June pooled), or entirely skipped (February absent) for the robustness of the data (Fig. 1). The morphological account of the female specimen collected during the study is summarized in Table 1.

### Collection of habitat and climatic parameters

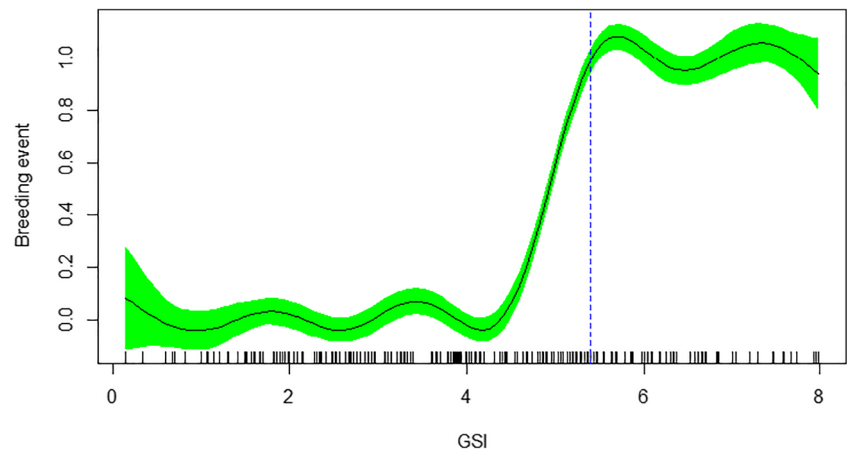
Simultaneously with fish sampling in wetlands, habitat parameters like air temperature (°C), surface water temperature (°C), Secchi disc transparency (cm), dissolved oxygen ( $\text{mg L}^{-1}$ ), free carbon dioxide ( $\text{mg L}^{-1}$ ), pH (units), total dissolved solids ( $\text{mg L}^{-1}$ ), specific conductivity ( $\mu\text{S cm}^{-1}$ ), total alkalinity ( $\text{mg L}^{-1}$ ), hardness ( $\text{mg L}^{-1}$ ), salinity ( $\text{mg L}^{-1}$ ), nitrate ( $\text{mg L}^{-1}$ ), and phosphate ( $\text{mg L}^{-1}$ ) were recorded using probes (multi-parameter Tester™ 35 series, EUTECH instruments OAKTON) or titrimetric procedures following standard methodologies (APHA 2012). The observed habitat parameters in the floodplain wetlands were tallied against the standard expected range published in Sarkar et al. (2020) and checked for any abnormality.

Region-specific monthly rainfall (mm) data was procured from weather stations under the Indian Meteorological Department (IMD), Alipore, India. Region-specific data on "long-term" changing air temperature patterns, annual rainfall, seasonal rainfall composition, and seasonal temperature pattern over the last three and half decades (1980–2015; also procured from IMD) were already analyzed in Karnatak et al. (2018). The estimates were also used here since the study region overlapped, and the progress of climatic trends is often slow. In terms of the seasonality of climatic data, three seasons were considered, i.e., pre-monsoon (January to April), monsoon (May to August), and post-monsoon (September to December) (Karnatak et al. 2018).

### Quantification of biological and fishing thresholds for breeding

Gonadosomatic index (GSI) is regarded as a proxy of spawning readiness in fishes, and it was calculated using the formula:  $\text{GSI} = (\text{GW} * 100) / \text{BW}$ , where GW is the fresh gonad weight (g),

**Fig. 1** Threshold gonadosomatic index (GSI = 5.4 units; intersection of red and blue dashed lines) for breeding of female *Gudusia chapra* in Gangetic floodplain wetlands. Black dashes on the x-axis indicate data points



and BW is the wet body weight (g) (Karnatak et al. 2018). Threshold GSI for spawning, hereinafter referred to as “breeding GSI,” was quantified using a generalized additive model (GAM) between GSI as an independent variable and breeding event (0 or 1) as a response variable (Karnatak et al. 2018). The binary coding strategy is defined in the supplementary material. Fulton’s condition factor (*K*), hereinafter referred to as fitness, was calculated using the formula:  $K = 100 \times (W/L^3)$ , where *W* is the body weight (g), and *L* is the total length (cm) (Froese 2006). Threshold fitness for spawning, hereinafter referred to as “pre-spawning fitness, ( $K_{\text{spawn50}}$ ),” was quantified using the Kaplan-Meier survival function with *K* as the independent variable and breeding event as the response variable (Sarkar et al. 2017). The total body length of the smallest female (mature/ripe) encountered in our dataset was considered as the first maturity size. Size at 50% maturity ( $L_{M50}$ ), i.e., threshold total body length beyond which there is at least 50% chance of encountering a breeding female, was quantified using the Kaplan-Meier survival function with total body length (independent variable) and breeding event (response variable) (Sarkar et al. 2018a).

A novel parameter coined as pre-spawning girth ( $\text{Girth}_{\text{spawn50}}$ ) was parameterized.  $\text{Girth}_{\text{spawn50}}$  is the body girth beyond which at least 50% of the females will spawn.  $\text{Girth}_{\text{spawn50}}$  includes the swollenness of the abdomen/belly of gravid females with mature-ripe ovaries inside, in contrast to the non-spawning individuals.  $\text{Girth}_{\text{spawn50}}$  was quantified using

the Kaplan-Meier survival function with girth as an independent variable and breeding event as the response variable. A back-validation of  $\text{Girth}_{\text{spawn50}}$  with  $L_{M50}$  was performed using a length-girth relationship (see supplementary material). The mean body girth of breeding females (mature and ripe) was also compared with that of the non-breeding ones (immature and maturing) to check whether there is any need to increase the mesh size demand. All analyses were done in RStudio v1.2.5.

### Identification and quantification of key environmental cues for breeding

An array of environmental parameters (13 parameters: air temperature, monthly rainfall, transparency, dissolved oxygen, free carbon dioxide, pH, total dissolved solids, conductivity, total alkalinity, hardness, salinity, nitrate, and phosphate) were presumed as the potential environmental cues for breeding. Through variance inflation factor (see supplementary material), the parameters were reviewed and solved for multicollinearity issues to avoid statistical biasedness in our subsequent analyses. Post variable curation, multiple GAM analyses (i.e., multivariate non-linear regression) were carried out with six non-linear predictor variables (water, rainfall, pH, alkalinity, hardness, and transparency) and one response variable (GSI) (Murase et al. 2009). Besides the predictive variables, the model was also incorporated with a linear variable called “breeding cycle” as a diagnostics factor. The dataset was coded as

**Table 1** Descriptive account of female *Gudusia chapra* sampled from floodplains in lower Gangetic plains (West Bengal, India). Data presented in range and mean ± standard deviation (in parentheses)

Total length (cm)	Body weight (gm)	Girth (cm) <sup>#</sup>	GSI (units)	Condition factor (units)	Growth coefficient ( <i>b</i> -value of LWR) <sup>##</sup>	Length-girth relationship
6.5–18 (11.4 ± 3)	3–43.5 (17.1 ± 10.5)	3.2–11 (5.8 ± 1.5)	0.15–8 (4.1 ± 1.9)	0.6–1.8 (1.1 ± 0.3)	2.47 (adj. $R^2 = 0.931, p < 0.01$ )	$\text{Girth} = 1.20 + (0.858 * \text{length})$ (adj. $R^2 = 0.7, p < 0.01$ )

<sup>#</sup> For calculating body depth, divide the body girth value by 2

<sup>##</sup> Calculated using log-transformed length-weight data of females and length-weight relationship (LWR)



breeding cycle 1 (data between 2017 and 2018) and breeding cycle 2 (2018 and 2019) to derive outputs that eliminate breeding cycle-specific variabilities (if any). Finally, the significant predictors ( $p$  value < 0.05) were identified as the “key” breeding cues.

The next step was to quantify the key breeding cues for inducing successful spawning (breeding) at the population level. Individual GAMs were plotted between the identified breeding cue (as predictor variable) and GSI (response variable). The plotted GAM function (curve) was visually inspected against the breeding GSI (as reference or benchmark), and the breeding cue thresholds were quantified where the curves fulfilled the breeding GSI requirement (Sarkar et al. 2019a, b). All analyses were done in RStudio v1.2.5 using the “mgcv” package. Any significant difference in GSI between breeding cycles 1 and 2 was assessed using a one-way ANOVA post hoc Tukey HSD test ( $\alpha$  level 0.05). Water temperature and rainfall variabilities between breeding cycles were statistically tested using  $F$ -test ( $\alpha$  level 0.05).

### Tracking shifts in breeding phenology

Based on the observed cycle of GSI across two consecutive breeding seasons, the present breeding phenology (onset, offset, peak, and duration of breeding) was assessed. Online published records ( $n = 5$ ) of the breeding season of *G. chapra*, limited to the available records from the studied region only (lower Gangetic basin, West Bengal, India, and Bangladesh), were searched and arranged chronologically (Kabir et al. 1998; Vinci et al. 2005; Rahman and Haque 2006; Mondal and Kaviraj 2010; Ahamed et al. 2014). A heatmap was generated for depicting chronological patterns in breeding phenology, using the ggplot2 package in RStudio v1.2.5.

## Results

### Description of biological, habitat, and climatic parameters

A descriptive account of the morphological and reproductive parameters of the females assessed (total length: 6.5–18 cm, bodyweight 3–43.5 g, girth 2.4–11 cm) is summarized in Table 1. Across the two breeding cycles studied, sexually matured females comprised 37.8% of the total females sampled. Compared to the non-breeding individuals, the gravid females usually have 110% higher GSI, 44.5% higher body weight, and 16.4% broader body girth, but 9.1% lower Fulton’s condition factor. No significant difference in GSI between the two breeding cycles ( $p > 0.05$ ) existed. The habitat parameters recorded during the sampling period are summarized in Table 2. The studied habitats’ meso-climatic conditions comprised 17.6–34.7 °C daytime surface water

**Table 2** Descriptive account of habitat parameters recorded in the studied floodplain wetlands of West Bengal, India

Parameters	Observed range
Water temperature (°C)	17.6–34.7
Monthly rainfall (mm)	0–434.4
Secchi disc transparency (cm)	6–183
Dissolved oxygen (mg L <sup>-1</sup> )	3.40–7.3
Free carbon dioxide (mg L <sup>-1</sup> )	0–5
pH (units)	7.4–9.4
Total dissolved solids (mg L <sup>-1</sup> )	191.4–633.7
Specific conductivity (µS cm <sup>-1</sup> )	272–775.3
Total alkalinity (mg L <sup>-1</sup> )	100.7–317.2
Salinity (mg L <sup>-1</sup> )	131.5–436.3
Nitrate (mg L <sup>-1</sup> )	0.01–0.38
Phosphate (mg L <sup>-1</sup> )	Trace–0.28

temperatures, 0–434 mm total monthly rainfall, and 11.7–12.2 h average day length. Across the two breeding cycles studied, water temperature did not vary significantly. However, significant variability ( $p < 0.05$ ) in rainfall was apparent between the two breeding cycles, with higher rainfall in 2018–2019 compared to 2017–2018.

During 1980–2015, the annual mean air temperature indicated a significant increasing trend ( $p < 0.05$ ). Compared to the base year 1980, it has increased by at least + 0.4 °C in recent times (2015–2018). The warming has been most noticeable during the monsoon months (May to August), with mean air temperature mostly staying above 30 °C. Rainfall indicated a statistically insignificant or erratic ( $p = 0.7$ ) decrease during 1980–2015. High inter-annual variability in rainfall exists, ranging from < 1000 to  $\approx$  2000 mm total rainfall per annum. The monsoonal rain (May to August) has also intensified by + 8.5% compared to 1980–1990. However, pre-monsoonal (January–March) or post-monsoonal (September–December) rainfall has decreased by 2.3 and 6.2%, respectively. The rainfall distribution is getting adjusted to a limited number of high-intensity rainy days within May–August.

### Biological, environmental, and fishing thresholds for breeding

For successful spawning, the females need to attain a threshold GSI of at least 5.4 units (adj.  $R^2$  0.9, GCV 0.02,  $p < 0.01$ ) (Fig. 1). In the descending order of priority, rainfall and water temperature and transparency were identified as key environmental cues ( $p < 0.05$ ) influencing GSI. Together, rainfall and water temperature could explain 48.9% of the deviance in GSI, highlighting the major influence to focus. The nature of the impact of temperature and rainfall on GSI was positive;

i.e., with increasing temperature and/or rainfall, the GSI most likely increases. An approximate linear budget is as follows:  $GSI = -1.13 \pm 0.77 + 0.003 \pm 0.001 * \text{rainfall} + 0.16 \pm 0.03 * \text{temperature}$ . The threshold rainfall for the attainment of breeding GSI was estimated to be at least 60–100 mm (adj.  $R^2$  0.44, GCV 2.03,  $p < 0.01$ ) (Fig. 2). The threshold water temperature for breeding was estimated to be at least 31–32 °C (adj.  $R^2$  0.24, GCV 2.69,  $p < 0.01$ ) (Fig. 3). No clear threshold could be identified for water transparency; GSI remained elevated within a wide range (4–110 cm) of transparency (adj.  $R^2$  0.21, GCV 2.87,  $p < 0.05$ ).

A weak and negative correlation was observed between Fulton’s condition factor ( $K$ ) and GSI (Pearson’s 2-tailed  $r = -0.14$ ,  $p < 0.05$ ). The negative correlation also stayed when  $K$  was derived from gonad weight subtracted body weight. Despite this, the parameter pre-spawning fitness ( $K_{\text{spawn50}}$ ) is presented for aiding future stock assessment studies.  $K_{\text{spawn50}}$  was estimated at  $K$  value range 1.29–1.54 units (Fig. S2). Climate preference for pre-spawning fitness attainment could not be identified because water temperature and rainfall showed no direct correlation with fitness. From the dataset, the first maturity (i.e., smallest mature female) was encountered at 6.8 cm ( $n = 3$ ); the second smallest mature female ( $n = 2$ ) was encountered at 7.3 cm total body length. Length at 50% maturity ( $L_{M50}$ ) was estimated at 14.1–15.4 cm—the length at which there is more than 50% probability of encountering a breeding female (supplementary Fig. S3).

The pre-spawning girth ( $\text{Girth}_{\text{spawn50}}$ , i.e., body girth at which there is > 50% probability of encountering a breeding female) was estimated at 7–7.4 cm (Fig. 4). Our data exhibited a median 22% increment in females’ body girth when they are ready to breed (interquartile range of girth: 5.4–7.4 cm) compared to the non-breeding ones (interquartile range of girth: 4.6–6.4 cm). For validation purposes, the length-girth regression (LGR) model (adj.  $R^2$ : 0.7,  $p < 0.01$ ) was estimated as follows:  $\text{Girth} = 1.2 + (0.4 * \text{length})$  (Table 1). Using  $L_{M50}$  estimates (14.1–15.4 cm) as input in this model, the projected girth at 50% maturity came out to be 6.8–7.4 cm. It is in close agreement with our  $\text{Girth}_{\text{spawn50}}$  estimates (7–7.4 cm). The

lowest overlapping value, i.e., 7 cm, was used for setting minimum mesh size recommendation. Therefore, any operational fishing net with mesh sizes below 7 cm will most likely trap and sieve out a breeding female during the breeding season—with more than 50% probability.

### Changes in breeding phenology

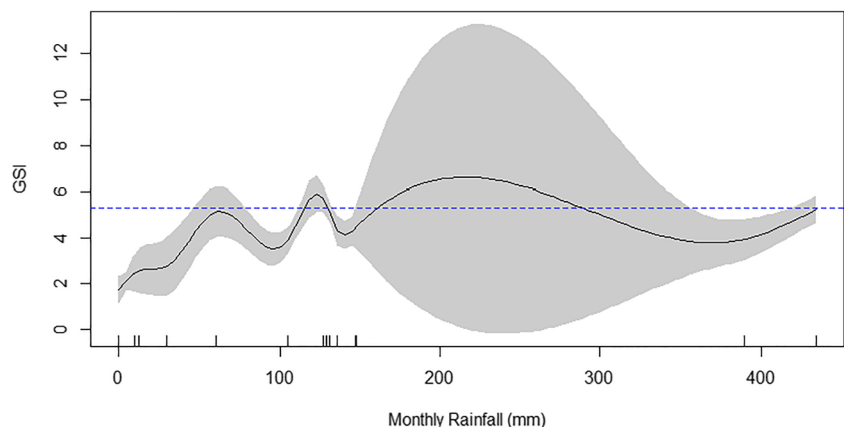
Based on the observed cycle of GSI, the breeding phenology of *G. chapra* was identified from April (start) to October (end), spanning up to 6 months. Based on the identified breeding GSI, breeding peaks were identified in May–June and September (Fig. 5), peaking GSI values beyond the threshold. We observed an intermittent break of maturity (or dampening of GSI) in August, probably because most of the females were spent post-spawning or re-maturing again to spawn in September as batch spawners. Rainfall was well above the required threshold during this period. Nonetheless, the historical comparison revealed consistency in Indian river shads’ breeding phenology over the last two decades (1998–2019) (Fig. 6). Accounting for any possible inter-study biasedness in reporting the breeding season’s start and end, we suspect no significant change in breeding phenology in the species.

## Discussions

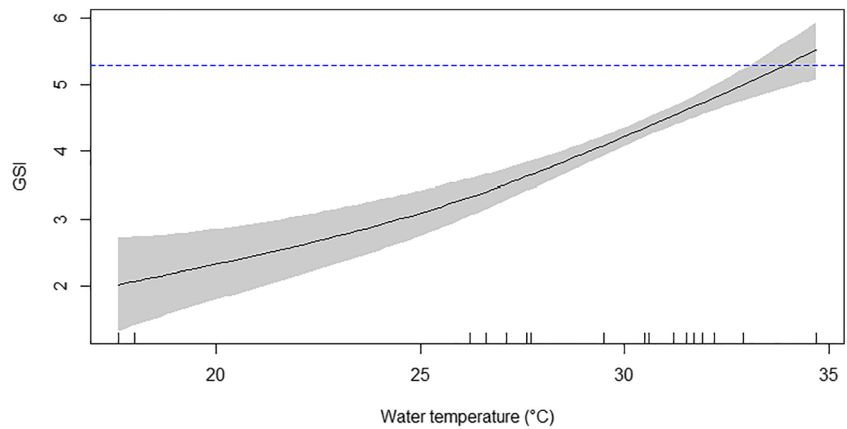
### Breeding thresholds

In the present study, we have quantified some breeding thresholds for Indian river shad females. Based on the published data available, some of our threshold estimates could be compared. For example, Hossain et al. (2010) estimated  $GSI > 4$  units could be roughly defined as a mature female. GSI values re-interpreted from data reported in Chondar (1977), Kabir et al. (1998), Mondal and Kaviraj (2010), and Ahamed et al. (2014) indicate GSI of 5–5.67 units in breeding females. In this light, our estimates of breeding GSI ( $\geq 5.4$  units) hold good. The case of size at first maturity is different. In the available data

**Fig. 2** Rainfall threshold (at least 60–100 mm) for breeding in female *Gudusia chapra* in Gangetic floodplain wetlands. Black dashes on the x-axis indicate data points. Horizontal blue dashed line indicates threshold GSI for breeding



**Fig. 3** Temperature threshold (above 31–32 °C) for breeding in female *Gudusia chapra* in Gangetic floodplain wetlands. Black dashes on the *x*-axis indicate data points. Horizontal blue dashed line indicates threshold GSI for breeding

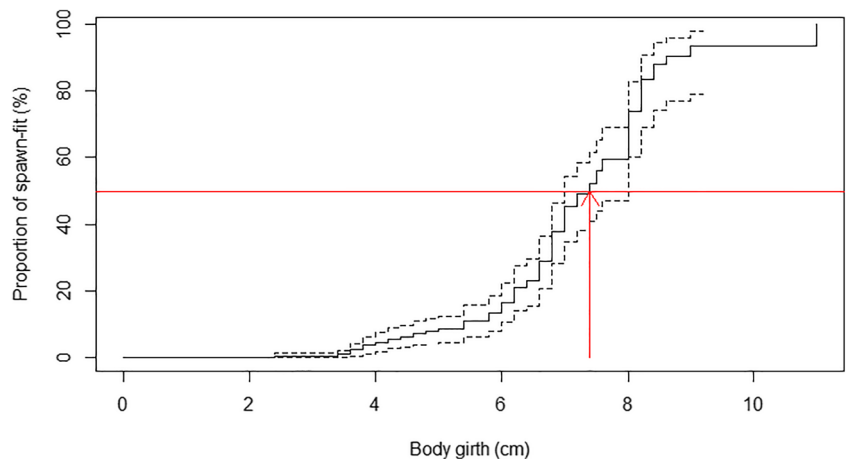


(Froese and Pauly 2019; Ahamed et al. 2014; Hossain et al. 2010; Kabir et al. 1998; Chondar 1977), females’ first maturity has been reported as 8–9.3 cm standard body length (SL). SL is the length from the snout to caudal peduncle. However, we have estimated total body length (TL). TL is measured from the snout to the end of the tail fin. As such, SL is always 1.7–2 cm lower than TL for the same fish (Ara et al. 2018; authors’ observation). Our first maturity estimate (6.8 cm TL), if converted, roughly corresponds to ~ 5.1 cm SL. The first maturity we observed was 6.8 cm TL or 5.1 cm SL, which is convincingly lower than reported so far. Even if we overlook the smallest mature females ( $n = 3$ ) at 6.8 cm TL in our dataset, six other females showed the first maturity between 7.3 and 7.7 cm TL (~ 5.6–6 cm SL). In total, we encountered a substantial 16 females, i.e., 19.8% of gravid females attaining first maturity (puberty) below 8 cm SL. When compared with existing records, these observations hint at earlier puberty than expected. Of course, the differences could have been due to the differences in sampling or sample coding approach used (Sarkar et al. 2018a), but this might not be the case. Based on available evidence, we suspect the females indeed are maturing at smaller sizes. From > 8 cm SL previously to 5.1 cm presently, a historical account of length at first maturity

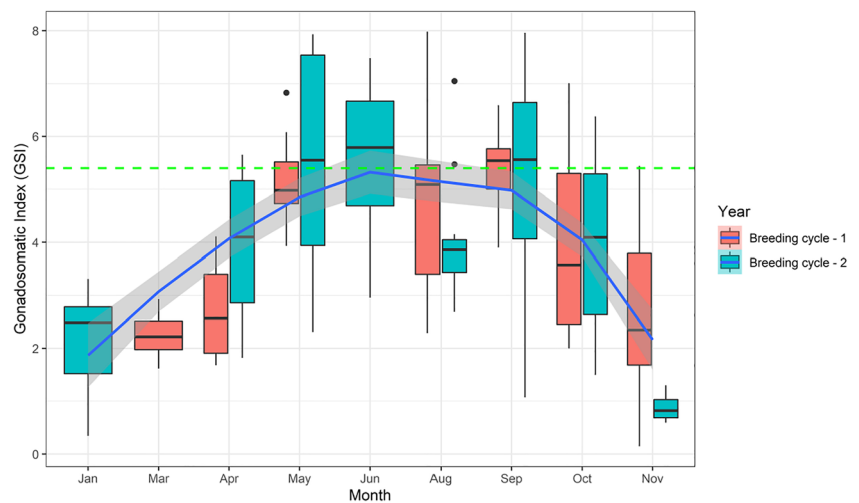
reported for regional females is depicted in Fig. 7. Whether this ~ 25–36% decrement in size at first maturity is due to a favorable trend of changing climate or fishery-driven selection is a subject of further validation. Follow-up investigations, repeated on the same species and localities, are required. *G. chapra* females are also less prone to skipped spawning decisions (Jørgensen et al. 2006). A detailed discussion can be found in the supplementary text.

The pre-spawning girth ( $Girth_{spawn50}$ ) was a novel parameter conceptualized in this study. To the best of our knowledge, the present estimate is the first one. Body depth measurements in the present study fell well within the species morphometric range reported in morphometric studies of *G. chapra*. Body depth can be 23.8–29.9% of TL (Ara et al. 2018; Arunachalam et al. 2015). The observed mean body depth (2.9 cm; Table 1) was 25.4% of the TL. Therefore, our girth estimates hold biologically true. The pre-spawning girth estimate also holds statistically true because it was successfully back validated with the length-girth relationship. Our  $Girth_{spawn50}$  estimate will most likely help formulate prudent conservation measures to safeguard the female breeding stocks against irresponsible fishing or overfishing per se.

**Fig. 4** Pre-spawning girth ( $Girth_{spawn50} = 7–7.4$  cm) of female *Gudusia chapra* stocks in Gangetic floodplain wetlands. Corresponds to responsible minimum mesh size recommendations



**Fig. 5** Annual maturity cycle of female Indian river shads (*Gudusia chapra*) in the lower Gangetic floodplains. Quartile plots (boxplots) indicate distribution of gonadosomatic index (GSI) through the calendar months (within the limits of sample availability), also visualized year or breeding cycle wise (wherever possible). The blue trend line represents the cycle of maturity. The horizontal green dashed line is the threshold GSI for breeding (5.4 units). Black dots represent outliers in the sample

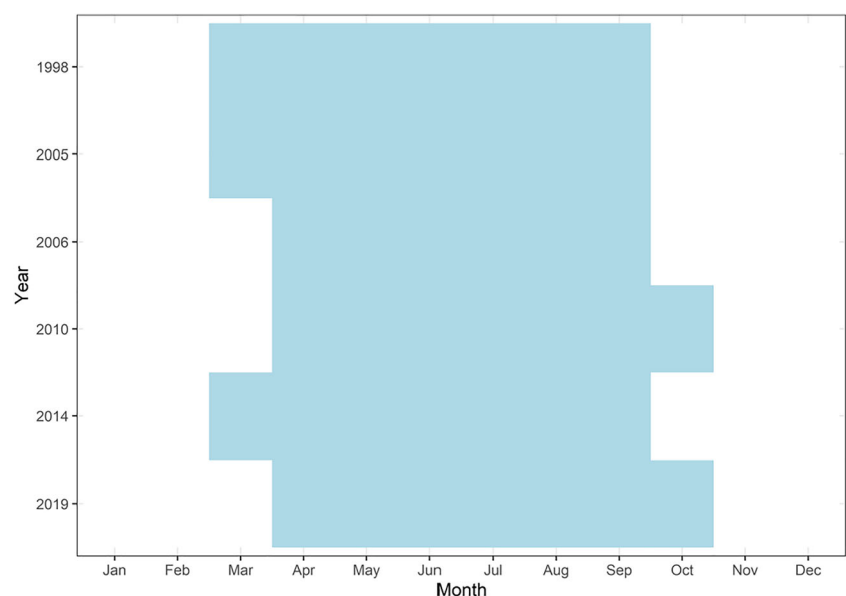


**Climatic influence on reproduction and size at maturity (puberty)**

The observed pattern of changing rainfall and temperature in the region is much inclined to fulfilling the required breeding thresholds of *G. chapra* females for the significant duration of the breeding season. During major parts of the breeding season, the rainfall or monsoonal rainfall (May to August) has intensified; warming of air temperature (cascading to water temperature) has been relatively intense during May to August (Kamatak et al. 2018; Sarkar et al. 2019a). It might have led to earlier maturity in females at smaller body sizes than previously estimated. However, the hypothesis seems valid in the context of existing evidence. Faster growth in enhanced thermal habitat (increased degree days due to warming) attributed to reduced length at maturity in Arctic cod (Jorgensen 1990). Increasing habitat temperature was

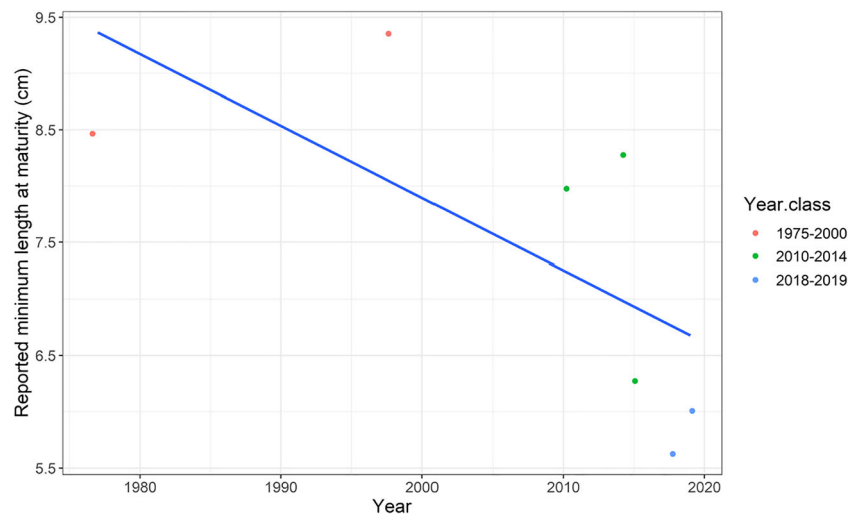
significantly related to decreased size at maturity in herrings (Hunter et al. 2019). Increased temperature-dependent growth over four decades decreased length at maturity in North Sea haddock (*Melanogrammus aeglefinus*) (Baudron et al. 2011). Neuheimer and Grønckjaer (2012) highlighted that reduction in size at maturity in North Sea Atlantic cod (*Gadus morhua*) was facilitated by intense fishing pressure under increasing sea surface temperatures but not by temperature alone. The fish population can reduce body size exclusively due to size-selective fisheries even when there is no prominent temperature rise (Hutchings and Reynolds 2004). It is also known as fishing gear-induced natural selection or fishing pressure-induced evolution (Heino et al. 2015). A recent report demonstrated that some of the studied habitats in the present work were slowly progressing towards a higher trophic state, corresponding to more algal biomass (Sarkar et al. 2020). It led to better food availability for *G. chapra*—an algal feeder

**Fig. 6** Chronologically arranged (1998 to 2019; top to bottom) breeding phenology of Indian river shad (*Gudusia chapra*) in the studied region, i.e., lower Ganges drainage. Light blue heatmap blocks indicate the span of breeding phenology. No significant and permanent distortion in the “block structure” indicates consistent breeding phenology over the years. Data: Kabir et al. (1998), Vinci et al. (2005), Rahman and Haque (2006), Mondal and Kaviraj (2010), Ahamed et al. (2014)





**Fig. 7** Reported minimum standard length at maturity in regional *Gudusia chapra* females over the years. Limited data exists and visualized as colored jitters according to year classes of samples collected in the studies. The indicative blue trendline is based on a generalized linear fitting and non-discriminative of methodological differences in individual studies. Data: Chondar (1977), Kabir et al. (1998), Hossain et al. (2010), Ahamed et al. (2014), Kumari et al. (2020), and the present study



(Rahman et al. 2008). Such circumstances, like better nutrition under higher temperatures, may reduce the size at maturity or advance puberty (Jonsson et al. 2013).

The primary reliance on rainfall for spawning in *G. chapra* females is much like their marine counterpart *Sardinella longiceps* in the Indian seas (Kripa et al. 2018; Jayaprakash 2002). A comparison with other freshwater fish species in the Indian subcontinent is provided in the supplementary text. The presently declining wild population trend of *G. chapra* cannot be attributed to climate change. The changing regional climate does not pose any significant threat to the breeding of Indian river shads in inland waters. Compared to historical records, the breeding phenology seems almost consistent over the last two decades (Fig. 6). However, variabilities in peak spawning timing exist (Kabir et al. 1998; Vinci et al. 2005; Rahman and Haque 2006; Mondal and Kaviraj 2010; Ahamed et al. 2014; present study), probably synchronized with inter-locality or inter-annual variabilities in rainfall. In extreme cases, the declining rainfall during September–October might lead to forced truncation of breeding, shortening the breeding phenology by – 2 months. Evidence of climate-induced skipped spawning decisions in clupeids has already been demonstrated in *Clupea harengus* (Engelhard and Heino 2006; Ojaveer et al. 2015).

**Influence of indiscriminative fishing on reproduction and size at maturity (puberty)**

Our data exhibited a median 22% increment in breeding females’ body girth than in non-breeding ones. It requires a mesh size “bigger than usual” to enable safe passage for the gravid fish without any obstruction. In this light, Girth<sub>spawn50</sub> was conceptualized. Presently, 1.5–10 cm mesh fishing nets are operational in their habitats, for example, seine nets (mesh range = 3.5–5 cm), cast nets (1.5–3 cm), lantern nets (2.5–3 cm), and gill nets (5–10 cm) (Sarkar et al. 2018b; Sandhya

et al. 2016, 2019; Das and Barat 2014). Many of these mesh sizes are clearly below the identified threshold, i.e., at least 7 cm mesh for allowing gravid females to swim through and successfully spawn. Fishing with finer mesh (< 5 cm) is done at least weekly and almost daily following heavy rains in June–July (Sarkar et al. 2018b; author observations). Reduced feeding intensity, lower body fitness, and bulged abdomen also make gravid females perform weaker escape maneuvers while being fished (non-quantified fishermen observations). Although such indiscriminative fishing pressure might sometimes be undetected, such actions repeated over generations have serious implications. Fisheries-induced evolution (FIE) can lead to earlier maturation through reduced length-at-age/maturity, progressively smaller body size (Shackell et al. 2010; Heino et al. 2015). Unchecked fishing mortality of spawning stocks can deter species recovery to independent environmental stressors like climate change (Hutchings et al. 2012; Tu et al. 2018). Reduction in body size or earlier puberty is a natural adaptation to avoid fishing or by-catch mortality (Hutchings and Reynolds 2004; Olsen et al. 2004), facilitated by favorable climate/food availability (discussed above). If ignored, it may lead to ultimate population collapse (Olsen et al. 2004).

When climate change and fishing pressure are weighed against life-history changes in fishes, fishing outweighs warming habitat (Tu et al. 2018; Neuheimer and Grønckjaer 2012; Hutchings and Reynolds 2004). Reductions in length at maturity in Scottish demersal fishes (Hunter et al. 2015), Baltic coastal pikeperch stocks (Lappalainen et al. 2016), multiple Pacific Salmon species in British Columbia (Ricker 1981), and West US or North Sea clupeid stocks (sardines, herrings, and sprats; Tu et al. 2018) have been argued to have been caused by indiscriminative fishing pressure, not by climate change. The collapse of Northern cod (*Gadus morhua*) fisheries (one of the worst collapses in fisheries history; Olsen et al. 2004) pointed out that fishes continually shifted towards

maturation at earlier ages and smaller sizes under FIE. This early maturation was an “early warning” sign, which was missed (Olsen et al. 2004). Whether the same phenomenon is setting-in for Indian river shads is a future research priority. The fecundity in *G. chapra* females is directly proportional to body length and girth (Narejo et al. 2006; Kabir et al. 1998). Therefore, any reduction in the size at maturity might lead to a concomitant decrease in fecundity and perhaps lowered offspring production. Even low egg quality (Jørgensen et al. 2006), with lowered yolk reserves, might reduce larval survivability. Fortunately, clupeids have demonstrated the ability to recover very well after a collapse if fishing pressure is released (Hutchings 2000). It might serve as a motivation to implement timely conservation measures.

### Conservation recommendations and summary for policymakers

The minimum mesh size for responsible fishing should ideally be  $\geq 7$  cm (or  $\geq 70$  mm mesh) during peak breeding months (May–June). When their habitats are fished almost daily following heavy rains in June–July, stringent mesh size compliance should be ensured. We proposed few advancements related to the conservation of small freshwater clupeid species in the tropical Asian inland waters, where length-girth regressions are utilized to fix responsible mesh size limits. Detailed information can be found in the supplementary material. The novel parameter coined as pre-spawning girth ( $G_{\text{spawn}50}$ ) might help protect the gravid females from overexploitation. Pre-spawning girth should be included in vulnerability assessments of declining fish stocks in natural waters.

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**Data availability** The data has been submitted along with the manuscript and can be found as supplementary material.

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**Ethics approval** All procedures performed in studies involving animals were in accordance with the ethical standards of the institution (ICAR-Central Inland Fisheries Research Institute).

**Consent to participate** Not applicable.

**Consent for publication** Not applicable.

**Conflict of interest** The authors declare no competing interests.

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