Fish diversity decline in the lower Gangetic plains: a victim of multiple stressors

Final accepted version, published in *Biodiversity and Conservation*; accepted 3 November 2022, first published online 22 November 2022. DOI: 10.1007/s10531-022-02505-7

Md. Taskin Parvez[1], ABM Mohsin[1], Sadman S. Arnob[2], Martyn C. Lucas[3], Nipa Chaki[1,4], Md. Abdul Gofur Khan[5ǂ], Shams M. Galib[1]

[1] Department of Fisheries, University of Rajshahi, Rajshahi 6205, Bangladesh

[2] Department of Soil, Water and Environment, University of Dhaka, Dhaka 1000, Bangladesh

[3] Department of Biosciences, University of Durham, Durham DH1 3LE, UK

[4] Department of Geography and Planning, University of New England, NSW, Australia

[5] Department Zoology, University of Chittagong, Chittagong, Bangladesh

[ǂ] Retired

Equal first authorship is accorded to MT Parvez and ABM Mohsin

Correspondence

Shams M. Galib

Postal address: Department of Fisheries, University of Rajshahi, Rajshahi 6205, Bangladesh

Email: thegalib@ru.ac.bd

ORCID identifier for Shams Galib http://orcid.org/0000-0001-7769-8150

ORCID identifier for Martyn Lucas https://orcid.org/0000-0002-2009-1785

DECLARATIONS

Funding: This study was supported by University of Rajshahi - University Grants Commission of Bangladesh (grant numbers A-621(5)/5/52/RU/Krishi-5/2013 and A-282-5/52/RU/Agri-17/17-18).

Conflict of interest: We declare we have no competing interests.

Availability of data and material: May be obtained on reasonable request from the corresponding author.

Code availability: May be obtained on reasonable request from the corresponding author.

Authors' contributions: MTP: Conducted the fieldwork and data curation; **ABMM:** Supervision of the study and acquisition of funding**, SSA:** Assisted with fieldwork; **MCL:** Participated in data analysis and writing the manuscript**; NC:** Conducted the fieldwork; **MAGK:** Critical review of the manuscript; **SMG:** Conducted the fieldwork, data analysis and led writing of the manuscript

Ethics approval: Not applicable.

Consent to participate: Not applicable.

Consent for publication: All authors read the manuscript and gave approval for the publication.

Acknowledgements: We thank Bangladesh Water Development Board and Bangladesh Meteorological Department for historical data. NC and MTP received fellowships from the Ministry of Science and Technology of the Bangladesh government.

Fish diversity decline in the lower Gangetic plains: a victim of multiple stressors

ABSTRACT

Analysis of long-term data provides a valuable approach to determining the extent of biodiversity decline and likely causes, but such approaches are rare in large tropical rivers. We investigated the response of the fish fauna to hydrological, climate and anthropogenic factors over the period 1982-2017 in the lower Ganges (Padma) River, Bangladesh. Systematic effort-based sampling of fish between 2007 and 2017 from a 70-km reach showed a decreasing trend in abundance and diversity. Compared to 1982 data for the same sites and fishing methods, 28 fish species, including 16 nationally threatened ones, were absent in recent catches, suggesting local extinction of these. Fish community diversity was negatively affected by fishing pressure (71 fishermen in 1980, 2616 in 2019, 37.8-fold increase) and non-native species abundance (6.8-fold increase in abundance between 2007 and 2017). Permanent water area has reduced by ~50% since 1984. Annual mean rainfall, Ganges water depth and river discharge at the study location decreased significantly since 1980 (by 19.2%, 17.8% and 27.6% respectively, while annual air temperature increased (25.1°C in 1981 to 26.2°C in 2019). Water diversion at the Farakka Barrage, ~70 km upstream, is partially responsible for reductions in permanent water area in the study reach. Potential sources of biological invasion and water pollution have been identified. Widespread ecological consequences on fish diversity and productivity, resulting from multiple factors, are occurring in the lower Ganges. Reduction of fisheries impacts and improved prevention of accidental aquaculture releases of non-native fishes are identified as conservation priorities for arresting the decline of native fishes in the lower Ganges.

Keywords: climate change, river barriers, fisheries, siltation, long-term data; hydrological trends

1 INTRODUCTION

Fresh water occupies less than 1% of the world's surface but supports ~10% of all known species, including 33% of vertebrates (Strayer and Dudgeon 2010). Biodiversity, including that of fishes, is declining at a faster rate in fresh water than in marine and terrestrial realms (WWF 2018; Reid et al. 2019) but its conservation does not receive sufficient attention in freshwater habitats (Dudgeon et al. 2006; Holland et al. 2012). Rivers are among the most severely affected freshwater ecosystems, because of their sensitivity to multiple anthropogenic activities (Suski and Cooke 2007; Vörösmarty et al. 2010). For smaller-scale freshwater habitats, such as streams and oxbows, human impacts on aquatic communities can be measured robustly in replicated treatment sites, comparing protected or pristine conditions with degraded habitat and/or exploited populations (Wilkinson et al. 2018; Barocas et al. 2021). When sampling is carried out over a short field campaign (Wilkinson et al. 2018; Barocas et al. 2021), a 'snapshot' view is generated. Long-term studies in specific localities can be valuable in identifying the trends of biodiversity change in relation to landscape-scale stressors including climate, pollution and exploitation (Counihan et al. 2018). Such approaches are well-suited to large rivers, where treatment replication may be difficult due to the large physical scale. Determining biodiversity change in relation to environmental conditions and conservation threats is important to ensure appropriate management (Reid et al. 2019), but long-term studies of this type have mostly been conducted in developed countries of Europe, North America and Australasia (Daufresne et al. 2004; Chessman 2009; Pont et al. 2015).

Several long-term ecological stressor studies have focused on the impacts of climate change on aquatic organisms or ecosystems (Daufresne et al. 2004; Chessman 2009). Other factors, such as exploitation, flow regulation, water pollution and biological invasions, also have strong potential to impact aquatic life adversely (Dudgeon et al. 2006; Grzybowski and Glińska-Lewczuk 2019). Therefore, studies which seek to determine the contributions of all potential factors on changes in ecosystem health indicators are desirable for effective conservation actions (Arthington et al. 2016).

Many of the most biodiverse freshwater systems across the world are large rivers in the tropics and subtropics, including the Amazon, Congo and Mekong (Dudgeon 2012; Winemiller et al. 2016). In several of these rivers, megafaunal declines have been observed (He et al. 2019). However, long-term records of abundance and diversity for indicator communities such as freshwater fishes are rarely available in the developing world, resulting in a lack of historical data (Comte et al. 2020). Nonetheless, many developing countries support rich biological diversity, but loss of biodiversity in these regions is also fast and has received inadequate research and conservation attention (Gopal 2005; Dudgeon 2012).

This statement may also be true for the Ganges (Das et al. 2013), one of the longest rivers in the world, flowing through India and Bangladesh, and globally known for its rich fish biodiversity (Welcomme 1985; Dudgeon 2000). The lower river supports at least 28 species of nationally/globally threatened fish as well as fish-dependent flagship megafauna, such as critically endangered gharial (*Gavialis gangeticus*), a crocodilian, and endangered Ganges river dolphin (*Platanista gangetica*) (IUCN Bangladesh, 2016; Joadder et al., 2015; Kelkar and Dey, 2020). Although several potential factors including different anthropogenic, climatic and biological threats have been identified for the declining and changing fish communities in the Ganges (Sarkar et al. 2012; Dey et al. 2020) no study has carried out a thorough analysis of these factors to date. The Ganges has an enormous role in agriculture, fisheries, transportation, culture and religion, and tourism in India and Bangladesh (see Kumar 2017 for details) and, therefore, any marked changes in the river's health may impact on these sectors in the region (Hassan 2019). Bangladesh supports rich biodiversity, including over 265 species of freshwater fishes (Rahman 2005). However, the freshwater fish fauna of Bangladesh, including in the lower Ganges floodplain, is affected by natural environmental variability and anthropogenic factors such as water level management (Halls et al. 1998, 1999; De Graaf 2003; Craig et al. 2004). Professional Bangladeshi fishermen commonly report a decline in fish capture from open waters (primarily rivers) in recent times (Galib et al. 2018a).

In this study, long-term changes in fish fauna in relation to anthropogenic, climatic and habitat factors are determined for the lower Ganges in Bangladesh. The study objectives were to (a) identify changes in fish species richness and diversity of the lower Gangetic plains over the long-term (since 1980), (b) determine long-term (since 1980) relationships between climatic, habitat and anthropogenic factors in the study area and the fish fauna and, (c) identify fish species, compared to historical data, that may have become extinct from the river in the study area. We hypothesised that the lower Ganges is suffering from multiple stressors which have negatively affected native fish species richness and abundance over time. We consider what actions need to be implemented most urgently to conserve the lower Gangetic plains ecosystem through the lens of the freshwater fish community.

2 MATERIALS AND METHODS

2.1 Study site

The River Ganges originates in the Gangotri glacier of the Himalayas and flows through India and Bangladesh. The 366-km long Bangladeshi section of the lower Ganges (Padma) is characterized by vast river floodplains and becomes increasingly brackish as it nears the coast. The hydrology and geomorphology of the lower Ganges is influenced by the Farakka Barrage (Mia et al. 2009) 18 km upstream of the India-Bangladesh border, and which, since 1975 has diverted a proportion of water to the Hooghly River and by a series of other canals. We collected fish samples at nine locations in the Bangladesh part of the Ganges spanning between Godagari and Sardah (24°27'42.4"N 88°13'21.6"E to 24°16'02.9"N 88°44'20.8"E, ~70-km long river reach) from 2007 to 2017 (Figure 1) and compared these with samples previously gathered in 1982 (Islam and Hossain, 1983). The study area is also considered a hotspot for globally threatened gharial and Ganges dolphin (IUCN Bangladesh, 2016). The reach can be considered representative of the whole lower Ganges River in Bangladesh in terms of flow types, bank-side features, land and water use patterns.

2.2 Assessment of changes in fish abundance and diversity

Fish fauna data were based on samples gathered monthly from July 1981 to June 1982 (hereafter referred to as 1982; reported in Islam and Hossain, 1983), 2007, 2012 and 2017 at the same nine sites (Figure 1) and using the same fishing gears. Sampling in 1982 provided presence-absence species information only. We conducted standardised monthly sampling in 2007, 2012 and 2017 using a combination of fishing gears (seine net, cast net and rectangular trap) considered effective in sampling fishes of different species and sizes in South Asian floodplain rivers across different water levels (Galib et al. 2018a, b). This yielded 324 samples in total [N = 9 (sites) ×12 (months) × 3 (years)]). At each sampling site, two seine nets (mesh 7×7 mm, 30×2.5 m), two cast nets (mesh 10×10 mm, $\pi \times 1.25^2$ m = 4.9 m^2) and four rectangular fishing traps '*Kholsun*' (mesh 25×20 mm, 0.8×0.75×0.1 m) were employed to collect fishes. Fishing nets were used during daytime, between 0600 and 1100 whereas fishing traps were set in the evening before the day of sampling and left overnight (~12 hours) in the water, in accordance with the local fishing practices. The cast nets were hauled 15 times at each site and the fishing duration was about 1.5 h. In order to standardise the sampling effort, all fishing gears were operated over the same time period on every sampling occasion. Collected fish were identified following standard literature (Rahman 2005) and classified after FishBase (Froese and Pauly 2019). Individuals, difficult to identify on site, were brought to the laboratory for identification; the rest were returned to the river. Global and national conservation status of fishes in this study are based on the 'Redlist databases' of IUCN (2020) and IUCN Bangladesh (IUCN Bangladesh, 2015) respectively. Two unconfirmed species (*Puntius* sp. and *Chanda* sp.)

reported in Islam and Hossain (1983) were excluded from our analyses. Taxonomic positions of the fish species, including those from 1982 and their corrections, are based on FishBase (Froese and Pauly 2019).

2.3 Determination of factors affecting the ecosystem and fish fauna

We considered the five broad categories of threats described by Dudgeon *et al.* (2006) responsible for declining freshwater biodiversity worldwide comprising (i) overexploitation, (ii) habitat degradation, (iii) flow modification, (iv) water pollution and (v) biological invasion to determine their impacts on fish fauna in the river. However, these categories are influenced by each other and component factors (e.g. water depth as a habitat component) may contribute/reflect multiple threat categories (e.g. habitat and fishing pressure).

2.3.1 Overexploitation

Most fishing in the study area originates locally. To determine the fishing pressure, and resultant risk of overexploitation, we conducted door-to-door surveys in 27 adjacent villages to our sampling sites (Figure 1) in 2019 to determine the number of fishermen in each village, and collected information on the past and present fishing practices (experience, types of gear used). During the survey every fisherman was asked to disclose the year in which they started fishing. To ensure accuracy, they were asked to recall memories (e.g. class in school, notable events in the year) relevant to the maiden fishing year, in order to cross reference and check the year. We also asked villagers to identify people who used to fish but left the study area to live elsewhere, or who no longer fished (e.g. had died). This allowed us to determine the total number of fishermen over time. For 2007, 2012 and 2017 it was possible to determine the number of fishermen (7-day average every sampling month, prior to our fish sampling day) per 500 m^2 area at every sampling site and this was used as a measure of fishing pressure. For this purpose, volunteers were employed to monitor the fishing activities from 0500–0700, 1000–1200 and 1600–1900 hours. These times were chosen as most local fishing takes place during these periods of the day.

2.3.2 Habitat degradation

Several factors, associated with physical changes of the habitat, were investigated. Historical (1980–2017) fortnightly water depth (average depth over the cross-section, recorded at Boalia, located within the study area) from the Bangladesh Water Development Board (BWDB), allowed us to compare temporal changes in water depth over time. Historical (1980–2019) daily rainfall, evaporation and air temperature (since 1981) data of the study area were collected from the Bangladesh Meteorological Department of the Bangladesh government. Yearly changes (1984–2019) in river channel permanent water areas were based on Landsat (NASA-USGS) satellite images of the study area, captured on 31 December every year. Being captured during the dry season (November–March), these satellite images represent the permanent water area. The driest period usually starts in November and continues until January (Galib et al. 2018a; Khan et al. 2022). Therefore, we chose 31 December as a reliable reference point of the peak drying period. Although many fish species in the lower Ganges rely on floodplain inundation for reproduction (Craig et al. 2004), they also rely upon permanent water in the main channels for refuge habitat during the dry season (Galib et al. 2018a).

2.3.3 Flow modification

The Farakka Barrage, located ~70 km upstream of the study area, is the only major structure that could affect the flow of Ganges in the study area. From BWDB, weekly water discharge data (1969–2019) of the study area were collected.

2.3.4 Water pollution

As municipal wastewater was the only potential local source of water pollution in the study area we recorded the location of drains that carry wastewater into the river. We measured water temperature, water transparency, dissolved oxygen (DO), pH, and total dissolved solids (TDS) monthly at the sites where fish were sampled (in 2007, 2012 and 2017). Water temperatures and DO were measured using a digital DO meter (model DO-5510, Lutron electronic); pH, TDS and water transparency were measured using a digital Hanna pH meter (model HI 8424), Hanna TDS tester (model HI 98301) and Secchi disk, respectively. Measurements were recorded at three locations (at 25%, 50% and 75% width of the channel) between 9.00 and 10.00 hours on each sampling day. We also included monthly biochemical oxygen demand (BOD) data, collected from the Department of Environment of the Bangladesh government, in the analysis. These measurements are useful indicators of oxygen-demanding organic pollution to which fishes can be sensitive. Both nitrate and phosphate can be an important indicators of eutrophication (Li et al. 2022) but these are not currently monitored in the Ganges in Bangladesh, so they were not considered here. In addition, seasonal (summer, monsoon and winter; recorded in late April, early July and mid-December respectively) data of DO, pH, water transparency and TDS were recorded at Boalia (between S5 and S6 sites) since 2001 and analysed for trends.

2.3.5 Biological invasion

Potential sources of non-native species were monitored between 2007 and 2019 and people involved in fish ranching in the river were interviewed (n = 4 in 2007, 7 in 2012, 8 in 2017; located between S4-S6) for relevant information such as accidental losses. Number of non-native fishes sampled each month (2007, 2012, 2017) was recorded.

2.4 Data analysis

2.4.1 Temporal changes in fish fauna

Long-term changes in fish species richness and species composition were generated from species presence-absence data from 1982, 2007, 2012, and 2017. Relative abundance data per species were available from 2007-2017. Linear mixed-effects modelling (LMM) was employed to analyse repeated measures fish abundance (all species combined) and species richness using the “lme4” (Bates et al. 2015) and “lmerTest” (Kuznetsova et al. 2016) packages of the R software (R Core Team 2020). During LMM, sampling years were tested as fixed effects and sampling sites and months were considered random effects. To determine the Bray-Curtis dissimilarity between fish communities over time, a Permutational Multivariate Analysis of Variance (PERMANOVA), using Bray-Curtis distance matrix and 999 permutations, was carried out using the ‘vegan’ package (Oksanen et al. 2018).

Non-metric Multidimensional Scaling (NMDS) (Kruskal and Wish 1978) ordination plots were generated to visualize temporal variation of fish communities using the “vegan” package, based on species presence-absence (for 1982, 2007, 2012, 2017) and abundance (for 2007, 2012, 2017) data (Oksanen et al. 2018). Multivariate Similarity Percentage (SIMPER) analysis, based on decomposition of the Bray–Curtis dissimilarity index (Clarke 1993), was used to determine the average per cent dissimilarity in fish community composition over time (2007 vs. 2012, 2007 vs. 2017 and 2012 vs. 2017).

2.4.2 Factors affecting fish fauna

We examined effects of fishing pressure, non-native fish abundance and seasonally changing environmental factors on fish abundance using LMM. Fish abundance (all species combined) data were summed across the nine sites for each month (2007, 2012, 2017) and used in the model as sampling site-based data were not available for several parameters (BOD, rainfall, evaporation and water discharge). Because water quality, hydrological and physical habitat variables considered in the study may be correlated with each other, a principal component analysis (PCA) was first performed and correlated factors were used as groups (as principal components) for further analysis (for PCA details see Table S1; Figure 2). Two PCA factors were identified (PC1, water temperature–BOD-evaporation-water transparency-rainfall-TDS; PC2, DO-pH-water discharge-water depth) for further analyses based on scree plots and a broken-stick model (MacArthur 1957). As our fish survey sample size was small (n=36), factors with a loading of >0.50 were considered to contribute to the meaning of a component (Budaev 2010; Galib et al. 2022; Shalehin et al. 2022). Therefore, the final LMM used for analysis contained fishing pressure, non-native fish abundance, two PCA factors (as PCA scores) and interactions of non-native fish abundance with PCA factors as these factors can affect non-native fishes in a habitat. Sampling month was considered a random factor in the model.

In addition, the long-term habitat (permanent water area, average water depth at Boalia), water quality parameters, hydrological (river discharge, rainfall) and climatic (air temperature increase, evaporation) data were also analysed in order to determine the extent and timescale of possible change in habitat and environmental conditions that could affect the fish fauna. Landsat satellite images (historical, 1984–2019) of the study stretch of the river were analysed using QGIS (version 3.12.2) to calculate the dry season water area and these values regressed against year. Long-term data (1980–2019) of fishing pressure, rainfall, air temperature, water discharge and water depth were analysed separately by regression models to identify their trends over time. For every parameter, data were subjected to possible regression models and diagnostic outputs (Table S2) and validation plots (Figure S1) were compared to select the best model and its type. Based on these, polynomial regression was found appropriate for fishing pressure, water discharge, water depth and permanent water area whereas, simple linear regression was selected for rainfall and air temperature (Table S1 and Figure S1).

Fish data were checked for normality before analysis and necessary transformations (square-root and log transformations for fish abundance and water quality data respectively; McDonald 2014) were made to meet the statistical assumptions for the tests. Normality of the model residuals was also checked with a q–q plot and no deviation from the linearity of the observations was observed.

3 RESULTS

3.1 Fish fauna

During the 2007–2017 surveys, 101 781 native fish of 77 species were captured (43 681 in 2007, 35 162 in 2012 and 22 938 in 2017) including 31 and 10 species of national and global conservation importance respectively (Tables 1 & S3). Eight non-native fish species were also recorded (Table S3). Comparisons with species richness data in 1982 showed that 28 native species were absent in fish samples during the 2007–2017 period, including 16 species of national conservation importance, represented by three critically endangered, five endangered, two vulnerable and six near threatened species (Table 2). Three species (*Anguilla nebulosa*, *Labeo nandina* and *L. pangusia*) were globally near threatened. Six native species were recorded in 2007–2017 but were absent in 1982 (Table S3). No non-native fish were reported in the study reach in 1982.

In 2007–2017, native species richness and abundance were dominated by the orders Cypriniformes (23 species, 29.0% relative abundance) and Siluriformes (21 species, 35.1% relative abundance (Table 1)). Abundance and species richness of native fish decreased and community structure altered over time (LMM for abundance and richness and PERMANOVA for community: all $p<0.001$; Table 3, Figure 3). Fish communities changed between 2007 and 2012 (SIMPER, Table S4, in which 38 species' relative abundance changed significantly); between 2012 and 2017 (SIMPER, Table S5 in which 48 species' relative abundance changed significantly); and between 2007 and 2017 (SIMPER, Table S6 in which 63 species' relative abundance changed significantly).

3.2 Factors affecting fish abundance

Fishing pressure and abundance of non-native fishes negatively affected native fish abundance (LMM: $p<0.05$; Table 4, Figure 4a & 4b). Significant effects of PC1 (Water temperature – BOD – Evaporation – Water Transparency – Rainfall - TDS) and interaction of non-native fishes with PC1 and PC2 (DO – pH – Water discharge – Water depth) affected the native fish abundance negatively and positively respectively (Figure 4, Table 4).

3.2.1 Fishing pressure

Across the 27 fishing villages surveyed in the study reach, the total number of professional fishermen increased (polynomial regression: $p<0.001$), by 3585%, from 71 in 1980 to 2 616 (~95% of the total households) in 2019 (Figure 5a).

3.2.2 Habitat modification and climatic factors

Historical rainfall data showed a decreasing trend (linear regression: $p<0.05$; daily mean 5.2 mm in 1980 to 4.2 mm in 2019; Figure 5b) in the study area, whereas the evaporation rate did not (Figure S2). Mean air temperature showed an increasing trend (Figure 5d), from 25.1°C in 1981 to 26.2°C in 2019. Decreasing trends in water depth (12.8 m in 1980-85 to 11.1 m in 2015-19), mean water discharge (6 008 $m^3 s^{-1}$ in 1980-85 to 4 581 $m^3 s^{-1}$ in 2015-2019) and permanent water area during the dry season (140 km^2 in 1984 to 70 km^2 in 2019) in the river were also recorded (Figures 5c, 5e, 5f & 6). Channel complexity has decreased over time (Figure 6).

3.2.3 Flow modification

Water discharge before (1969–1974) operation of the Farakka Barrage (mean and SD; 9 032 ± 12 084 $m^3 s^{-1}$) was significantly higher than during the barrage operation period (1975–2019; 5 146 ± 10 259 $m^3 s^{-1}$) (Welch t-test: $t = 4.3$, $df = 192.3$, $p < 0.001$). Dry-season discharge before (3 685 ± 1 473 $m^3 s^{-1}$) was significantly higher than during the barrage operation period (2 033 ± 1 636 $m^3 s^{-1}$) (Figure S3). During the monsoon (June–August), average discharges were 12 115 and 10 827 $m^3 s^{-1}$ prior to, and during, the barrage operation periods respectively.

3.2.4 Water pollution

Eighteen major drains (mean width 1.1±0.3 m) carrying wastewater from Rajshahi City and adjacent areas directly into the river, without any prior treatment, were recorded. No mass fish kills were recorded during the study period. Levels of DO, pH, water transparency and TDS in the Ganges study area between 2001 and 2019 showed no significant trend (linear regression: all $p > 0.05$; Figure S4).

3.2.5 Non-native fishes

Six non-native species were recorded in 2007 and 2012 sampling (Table 1). This figure increased to eight in 2017. Non-native fish abundance increased by 1131% between 2007 and 2017 (Table S3).

For about two decades, aquaculture of non-native fish species in cages and pens has occurred in Ganges River habitat in Bangladesh. This includes culture of predatory African sharptooth catfish *C. gariepinus*, a banned species in Bangladesh. This occurs during the dry season, when parts of the river become fully or partially separated from the main channel, and accidental escape is common (Figure S5). The most notable escape of this species was in 2016 when 3500 African sharptooth catfish, each ~1 kg, escaped from the rearing facility due to early monsoon flooding. In other years, the escape of at least 500 individuals was reported. At least 35 fishermen reported that they caught large African sharptooth catfish, believed to be escapees (Figure S5).

4 DISCUSSION

This study provides evidence that the abundance and species richness of native fishes in the lower River Ganges, Bangladesh, have decreased in recent years. Significant effects of fishing pressure, non-native species abundance, water quality and climatic parameters and their interactions on native fish diversity during 2007–2017 indicate that long-term changes in these have the potential to adversely affect the lower Ganges fish fauna. Our study contributes an example of the utility of consistent long-term data from river biodiversity indicator communities in the developing world, previously identified as scarce (Comte et al. 2020). The rapid decline in native species richness and relative abundance in the lower Ganges suggests that conservation actions need to be implemented in the near future if the integrity of the fish fauna of the lower Gangetic plains is to be maintained.

4.1 Changes in the fish community

Comparison against historical fish data suggests a rapid local extinction rate of fish species; 28 species were not found during 2007–2017 fish surveys at the same locations and using the same methods, but were available in

1982 (Islam and Hossain, 1983), while just six native species detected between 2007-2017 were not detected in 1982. It is also evident that most (~60%) of the species that have disappeared are threatened with extinction in the country (IUCN Bangladesh, 2015). Among the three critically endangered species, *Labeo nandina* and *Channa barca* have probably become extinct from Bangladeshi waters as there is no occurrence report of these two species since 1989 (Rahman 2005). Loss of suitable habitat and overexploitation are regarded as key factors for the threatened status of all these species (IUCN Bangladesh, 2015). This may also be true for the Ganges, where significant changes in river conditions have been recorded (this study; WII-NMCG, 2019). It is clear that, based on ~35 years' data, threatened fishes are disappearing and non-natives are increasing in the lower Ganges, a common pattern recorded in a habitat when invaded by non-natives (Haubrock et al. 2020; Galib et al. 2021).

4.2 Fishing pressure

The progressive increase of fishermen in the study area poses a major threat to the fish biodiversity, reflected in this study (significant negative effect of fishing pressure on measured fish abundance) and is also a key factor identified in the lower Ganges upstream of the Farakka Barrage (Dey et al. 2020). As licences are not required by fishermen in Bangladesh. it has become a common practice in the study area, as well as in other parts of the country, that more people are engaged in fishing every year. This is also because of the availability of modern fishing nets and vessels which make fishing much easier and a less risky job in recent times compared to the situation a few decades ago. The main control of fisheries activities in the lower Ganges is by regulation of fishing gears (Kelkar and Dey 2020), but Bangladeshi fishers frequently use illegal fishing gears and methods which are effective in capturing fishes irrespective of size and kind (Sultana and Islam 2016). Irregular or limited monitoring of illegal fishing by the controlling authority may also be responsible for the continuation of this illegal activity.

4.3 Habitat modifications and climatic factors

Impacts of climate change (Brander 2007; Pörtner and Peck 2010; Servili et al. 2020) and habitat modification (Lucas and Baras 2001; Dudgeon et al. 2006; Wilkinson et al. 2018) on aquatic life and ecosystems are widely recognised. Loss of permanent water area of the lower Ganges is partly due to water diversion at the Farakka Barrage which has significantly affected the dry season water discharge in the main Ganges channel downstream (Hassan 2019). A significant decrease in local rainfall, but unchanged evaporation rate over time, may also have contributed to the reduced water depth in the study area, leading to the loss of permanent water area. Although, increasing historical rainfall has been recorded for parts of Bangladesh (Shahid 2010) it can vary across regions (Guhathakurta and Rajeevan 2008) and a decrease may be the case for the study area, which is a part of the climate-vulnerable, drought-prone Barind tract region, characterised by low rainfall (Hossain et al. 2009). Air temperature has also increased. All these have the potential to influence local fish biodiversity. Almost all the freshwater fish species in the lower Gangetic plains breed during the monsoon season, in which heavy rainfall and water flow play a key role (De Graaf 2003; Rahman 2005), a recruitment pattern reported in many tropical floodplain rivers (Welcomme 1985; Lucas and Baras 2001; De Graaf 2003). Many deeper parts of the lower Ganges become completely or partially separated during the dry season. In these areas many fishes, especially those of a burrowing nature, take refuge and may exhibit aestivation (e.g. *Heteropneustes fossilis*). They are indiscriminately harvested by both professional and subsistence fishermen, resulting in poor carry over to the next breeding season (Galib *et al.*, 2018b).

There is no water-flow modifying structure in the study area or further downstream, but the Farakka Barrage may have adversely impacted habitat downstream of it, including in our study reach. Dewan et al. (2017) found that despite substantial planform change in the lower Ganges between 1973 and 2011, overall river-bank erosion was relatively balanced with accretion, with these processes largely driven by flood frequency and intensity which have remained broadly unchanged. However, the barrage, commissioned in 1975, is largely blamed for reduced freshwater supply to, and fish production in, the Bangladeshi part of the Ganges (Payne et al. 2004). During the dry season, an increased proportion of flow is diverted by the Farakka Barrage to the Hooghly River towards Kolkata (Dewan et al. 2017b). Although based on a few years' data before the opening of the barrage in 1975, our study shows that the annual water discharge of the Ganges, in the vicinity of Rajshahi, reduced by 43% compared to prior to barrage operation. However, a 90% reduction in the supply of freshwater via the Ganges to the Ganges delta, compared to that in the 1960s, has been estimated by some (Islam and Gnauck, 2011) and this is believed to be one of the key reasons for siltation downstream in the Bangladeshi Ganges. This has wider implications for the Bangladesh fisheries as the extensive floodplains of the country, the major natural breeding and feeding sites for native fishes, are fed mainly through complex river networks. Hence, reduced flow may have caused serious damage to the habitats and fisheries resources in Bangladesh (Galib *et al.*, 2018b), especially during the dry season when fish are reliant upon accessing adequate refuge habitat. It should be noted that there is a long-lasting conflict between Bangladesh and India over flow regulation of the Ganges (Dudgeon 2000). A lack of fish data prior to instalment of the Farakka Barrage has made it impossible to fully determine the impacts of this water regulatory structure on the fish community, although a steep decline in abundance of diadromous hilsa shad *Tenualosa ilisha* upstream of the barrage has been reported since the construction of Farakka Barrage (Das et al. 2013; Dey et al. 2020). Nevertheless, erosion-siltation processes associated with changes to channel planform of the lower Ganges occur on a large spatial scale of tens of kilometres (Dewan et al. 2017b). Therefore, it is possible that the observed reduction of dry-season habitat and average Ganges channel depth at Rajshahi, and likely to be contributing to the decline in native fish biodiversity there, is a reach-specific phenomenon over the observed study timescale. Therefore, similarly high-quality and long-term fish sampling, combined with environmental analysis, needs to be carried out on other large-scale reaches of the lower Gangetic plains to confirm landscape-scale declines of fish biodiversity and their causes.

4.4 Water pollution

The most common source of water pollution in Bangladesh is industrial effluent (Khan et al. 2022), but there is no major industrial development discharging to the Ganges immediately upstream of, or in the locality of, the study reach. However, the local administrative authority and Bangladesh government is planning an economic zone, with industry and a nuclear power plant near the bank of the lower Ganges that may impact water quality (Saha et al. 2018). Although there have been no reports of mass fish kills due to urban wastewater outfalls in the study area, lower abundance and species richness have been reported near the drains by fishermen. The lack of obvious fish kills may be due to the large river channel (3–5 km wide) and resultant large dilution effect, as smaller rivers in the locality suffered from fish population decline and mass fish kills (Galib et al. 2018b). Water quality parameters like DO, pH, water transparency and TDS did not vary significantly over years in the Ganges at Rajshahi; they were within the suitable levels for fishes (DoE 2014). Similar conclusions have been drawn regarding levels of heavy metals in sediments and surface water of the Ganges (Haque et al. 2019). Although water pollution is not yet a major threat to the river's biodiversity, it may become a problem soon and should be monitored carefully. Eutrophication can be a common modifier of freshwater ecosystems (Li et al. 2022) yet plant growth-limiting nutrients such as nitrate and phosphate are not widely monitored in Bangladeshi rivers, so we recommend that monthly sampling is carried out over the long-term at a network of sites across large rivers (including the Ganges), lakes and wetlands in Bangladesh.

4.5 Biological invasions

Although a negative relationship between non-native fish abundance and native fish diversity was evident, this may not currently be a direct effect of non-natives, and is more likely driven by the decrease in native fish diversity resulting from fishing pressure and wider environmental perturbations. Non-native fish were unrecorded in the study area in 1982 (Islam and Hossain, 1983). Non-native fish abundance in the Bangladeshi lower Ganges is still low compared to native fishes, but rapidly increasing; non-native species comprised ~0.4% of fish abundance in 2007, and ~4.4% in 2017, an 11.3-fold increase. This increase seems linked to local aquaculture, which developed for most of these species after 1982 (Galib and Mohsin 2011). In the lower Ganges, aquaculture species often escape during the monsoon period (primarily June–August but often extends into September) when flooding often damages the floating aquaculture cages. Ranching of non-native fishes in rivers of Bangladesh is common practice and has been reported from one of the anabranches of the lower Ganges, the Baral River (Galib et al. 2018a) and is mostly done by influential people illegally, or sometimes facilitated by government organisations. In Bangladesh, like many other developing countries, fish production receives priority over native fish conservation (Jones et al. 2021).

Until now, threats from non-native species have been considered unimportant for the loss of aquatic biodiversity in Bangladesh, but their impacts can be a key driver for declining biodiversity (Caffrey et al. 2014; Haubrock et al. 2020; Galib et al. 2021). Surprisingly, the African sharptooth catfish, continues to be reared in the lower Ganges floodplain, posing a high risk of biological invasion. Escape of these fishes in large numbers is common. The Bangladesh government banned this species because it is a voracious predator and a major threat to native species. Of the other non-native species, *Cyprinus carpio*, *Ctenopharyngodon idella*, *Hypophthalmichthys molitrix*, *H. nobilis* and *Oreochromis niloticus* are among the most frequently introduced aquatic species in the world (García-Berthou et al. 2005). Tilapia (*O. niloticus*), in particular, may pose a greater threat to the native biodiversity of the lower Ganges because of their prolific breeding. All the non-native species, except *Pterygoplichthys disjunctivus*, a locariid catfish, which has escaped from the ornamentals trade and become naturalised, have considerable demand as food fishes. Therefore, high fishing pressure may play a role in offsetting impacts of non-natives. Nevertheless, further initiatives must be considered to control or halt non-native species spread in the river.

4.6 Concluding remarks

The Ganges is an important river for aquatic biodiversity (WII-NMCG 2019; He et al. 2019), supports the livelihoods of millions of people (Kumar, 2017) and is suffering from multiple interacting stressors, a situation that poses the greatest conservation challenges (Arthington et al. 2016). Therefore, immediate measures to minimise the impacts of the various stressors to the Ganges downstream of the Farakka Barrage are needed, which will also be helpful for supporting 31 fish species of national and global conservation importance.

Climate impacts are difficult to overcome at a local scale, but other stressors should be managed carefully in order to minimise the existing or future effects on native communities.

The highest priority needs to be on reducing fishing pressure and damaging fishing practices, yet the level of fisheries enforcement is currently very low. We recommend the implementation of a fishing license fee to increase local enforcement. In parallel, we recommend that a fishing closed season, and local no-take-zones (NTZs), are instituted. As almost all the fish species in the region breed during the monsoon (June–August; Rahman, 2005) it may be easier to put such closed-season restrictions in place. Because most fishes retreat to the permanent parts of the Ganges and other large rivers during the dry season, NTZs or other types of protected area may prove helpful in local fish conservation. The use of protected areas is gaining traction in freshwater biodiversity conservation (Suski and Cooke 2007). There might also be wider benefits in such actions for conservation of fish-dependent flagship megafauna such as gharial and Ganges dolphin (IUCN Bangladesh, 2016; Kelkar and Dey, 2020). Currently a nation-wide ~20-day fishing ban on hilsa (*Tenuslosa ilisha*) is in practice in October/November, but in isolation this is unlikely to be beneficial for most at-risk fish species. Nevertheless, with an increasing human population, any attempt to reduce reliance on fishing will require alternative livelihood options for the fishermen. To date, aquaculture has been one option but, as is apparent above, insufficiently regulated aquaculture and ranching of non-native fishes is now putting the lower Ganges fish community at risk. Stronger policing and community education is needed around the risks of non-native species from aquaculture and the ornamental trade (Hossain et al. 2018; Ju et al. 2020). Once fully established, given the size of the Ganges, it would be almost impossible to control or eradicate non-natives.

With regard to water pollution, as municipal wastewater is the primary pollution source in the study area we suggest reed bed treatment or pre-treatment of wastewaters before discharge into the river. The former may be the best option due to local availability of adequate reed.

Vulnerabilities of freshwater habitats and their biota to different stressors are widely recognised but evidence from developing countries is rare, mostly due to a lack of historical data and systematic studies (Comte et al., 2020). This study contributes to bridging this gap in knowledge. We find that long-term ecological consequences of human impacts are occurring in the lower Ganges and that a combined understanding of potential causative factors, as produced in this study, is essential for appropriate conservation actions (Dudgeon 2011). We encourage the publication and analysis of other long-term data sets concerning biodiversity in subtropical regions, including southern Asian rivers, in order to determine commonalities in patterns and threats across the region.

REFERENCES

Arthington AH, Dulvy NK, Gladstone W, Winfield IJ (2016) Fish conservation in freshwater and marine realms: status, threats and management. Aquat Conserv Mar Freshw Ecosyst 26:838–857. https://doi.org/10.1002/aqc.2712

Barocas A, Araujo Flores J, Alarcon Pardo A, et al (2021) Reduced dry season fish biomass and depleted carnivorous fish assemblages in unprotected tropical oxbow lakes. Biol Conserv 257:109090. https://doi.org/10.1016/j.biocon.2021.109090

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models using lme4. J Stat Softw 67:. https://doi.org/10.18637/jss.v067.i01

Brander KM (2007) Global fish production and climate change. Proc Natl Acad Sci 104:19709–19714. https://doi.org/10.1073/pnas.0702059104

Budaev S V. (2010) Using principal components and factor analysis in animal behaviour research: caveats and guidelines. Ethology 116:472–480. https://doi.org/10.1111/j.1439-0310.2010.01758.x

Caffrey J, Baars J-R, Barbour J, et al (2014) Tackling invasive alien species in Europe: the top 20 issues. Manag Biol Invasions 5:1–20. https://doi.org/10.3391/mbi.2014.5.1.01

Chessman BC (2009) Climatic changes and 13-year trends in stream macroinvertebrate assemblages in New South Wales, Australia. Glob Chang Biol 15:2791–2802. https://doi.org/10.1111/j.1365-2486.2008.01840.x

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Austral Ecol 18:117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x

Comte L, Carvajal-Quintero J, Tedesco PA, et al (2020) RivFishTIME: A global database of fish time-series to study global change ecology in riverine systems. Glob Ecol Biogeogr geb.13210. https://doi.org/10.1111/geb.13210

Counihan TD, Waite IR, Casper AF, et al (2018) Can data from disparate long-term fish monitoring programs be used to increase our understanding of regional and continental trends in large river assemblages? PLoS One 13:e0191472. https://doi.org/10.1371/journal.pone.0191472

Craig JF, Halls AS, Barr JJF, Bean CW (2004) The Bangladesh floodplain fisheries. Fish Res 66:271–286. https://doi.org/10.1016/S0165-7836(03)00196-6

Das MK, Sharma AP, Vass KK, et al (2013) Fish diversity, community structure and ecological integrity of the tropical River Ganges, India. Aquat Ecosyst Health Manag 16:395–407. https://doi.org/10.1080/14634988.2013.851592

Daufresne M, Roger MC, Capra H, Lamouroux N (2004) Long-term changes within the invertebrate and fish communities of the Upper Rhone River: effects of climatic factors. Glob Chang Biol 10:124–140. https://doi.org/10.1046/j.1529-8817.2003.00720.x

De Graaf G (2003) Dynamics of floodplain fisheries in Bangladesh, results of 8 years fisheries monitoring in the Compartmentalization Pilot Project. Fish Manag Ecol 10:191–199. https://doi.org/10.1046/j.1365-2400.2003.00339.x

Dewan A, Corner R, Saleem A, et al (2017a) Assessing channel changes of the Ganges-Padma River system in Bangladesh using Landsat and hydrological data. Geomorphology 276:257–279. https://doi.org/10.1016/j.geomorph.2016.10.017

Dewan A, Corner R, Saleem A, et al (2017b) Assessing channel changes of the Ganges-Padma River system in Bangladesh using Landsat and hydrological data. Geomorphology 276:257–279. https://doi.org/10.1016/j.geomorph.2016.10.017

Dey S, Choudhary SK, Dey S, et al (2020) Identifying potential causes of fish declines through local ecological knowledge of fishers in the Ganga River, eastern Bihar, India. Fish Manag Ecol 27:140–154. https://doi.org/10.1111/fme.12390

DoE (2014) River water quality report 2013-2018. Department of Environment, Ministry of Environment and Forests, Dhaka, Bangladesh

Dudgeon D (2012) Threats to freshwater biodiversity globally and in the Indo-Burma Biodiversity Hotspot. In: Allen DJ, Smith KG, Darwall WRT (eds) The status and distribution of freshwater biodiversity in Indo-Burma. IUCN, Cambridge, UK, pp 1–28

Dudgeon D (2000) Riverine biodiversity in Asia: a challenge for conservation biology. Hydrobiologia 418:1–13. https://doi.org/https://doi.org/10.1023/A:1003998519910

Dudgeon D (2011) Asian river fishes in the Anthropocene: threats and conservation challenges in an era of rapid environmental change. J Fish Biol 79:1487–1524. https://doi.org/10.1111/j.1095-8649.2011.03086.x

Dudgeon D, Arthington AH, Gessner MO, et al (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. Biol Rev 81:163. https://doi.org/10.1017/S1464793105006950

Froese R, Pauly D (2019) FishBase. World Wide Web electronic publication. www.fishbase.org, version (12/2019).

Galib SM, Findlay JS, Lucas MC (2021) Strong impacts of signal crayfish invasion on upland stream fish and invertebrate communities. Freshw Biol 66:223–240. https://doi.org/10.1111/fwb.13631

Galib SM, Lucas MC, Chaki N, et al (2018a) Is current floodplain management a cause for concern for fish and bird conservation in Bangladesh's largest wetland? Aquat Conserv Mar Freshw Ecosyst 28:98–114. https://doi.org/10.1002/aqc.2865

Galib SM, Mohsin ABM (2011) Cultured and ornamental exotic fishes of Bangladesh: past and present. LAP LAMBERT Academic Publishing, Germany

Galib SM, Mohsin ABM, Parvez MT, et al (2018b) Municipal wastewater can result in a dramatic decline in freshwater fishes: a lesson from a developing country. Knowl Manag Aquat Ecosyst 37. https://doi.org/10.1051/kmae/2018025

Galib SM, Sun J, Twiss SD, Lucas MC (2022) Personality, density and habitat drive the dispersal of invasive crayfish. Sci Rep 12:1114. https://doi.org/10.1038/s41598-021-04228-1

García-Berthou E, Alcaraz C, Pou-Rovira Q, et al (2005) Introduction pathways and establishment rates of invasive aquatic species in Europe. Can J Fish Aquat Sci 62:453–463. https://doi.org/10.1139/f05-017

Gopal B (2005) Does inland aquatic biodiversity have a future in Asian developing countries? Hydrobiologia 542:69–75. https://doi.org/10.1007/s10750-004-5736-8

Grzybowski M, Glińska-Lewczuk K (2019) Principal threats to the conservation of freshwater habitats in the continental biogeographical region of Central Europe. Biodivers Conserv 28:4065–4097. https://doi.org/10.1007/s10531-019-01865-x

Guhathakurta P, Rajeevan M (2008) Trends in the rainfall pattern over India. Int J Climatol 28:1453–1469. https://doi.org/10.1002/joc.1640

Halls AS, Hoggarth DD, Debnath K (1998) Impact of flood control schemes on river fish migrations and species assemblages in Bangladesh. J Fish Biol 53:358–380. https://doi.org/10.1111/j.1095-8649.1998.tb01037.x

Halls AS, Hoggarth DD, Debnath K (1999) Impacts of hydraulic engineering on the dynamics and production potential of floodplain fish populations in Bangladesh. Fish Manag Ecol 6:261–285. https://doi.org/10.1111/j.1365-2400.1999.tb00080.x

Haque MA, Jewel MAS, Hasan J, et al (2019) Seasonal variation and ecological risk assessment of heavy metal contamination in surface waters of the Ganges River (Northwestern Bangladesh). Malaysian J Anal Sci 23:. https://doi.org/10.17576/mjas-2019-2302-14

Hassan ABME (2019) Indian hegemony on water flow of the Ganges: sustainability challenges in the southwest part of Bangladesh. Sustain Futur 1:100002. https://doi.org/10.1016/j.sftr.2019.100002

Haubrock PJ, Pilotto F, Innocenti G, et al (2020) Two centuries for an almost complete community turnover from native to non-native species in a riverine ecosystem. Glob Chang Biol gcb.15442. https://doi.org/10.1111/gcb.15442

He F, Zarfl C, Bremerich V, et al (2019) The global decline of freshwater megafauna. Glob Chang Biol 25:3883–3892. https://doi.org/10.1111/gcb.14753

Holland RA, Darwall WRT, Smith KG (2012) Conservation priorities for freshwater biodiversity: the key biodiversity area approach refined and tested for continental Africa. Biol Conserv 148:167–179. https://doi.org/10.1016/j.biocon.2012.01.016

Hossain MA, Mohsin ABM, Galib SM, et al (2009) Potentials of khas (public) ponds and kharis (canals) in Barind tracts: sustainable rural livelihoods in the face of climate change. Bangladesh J Progress Sci Technol 7:49–52

Hossain MY, Vadas R, Ruiz-Carus R, Galib SM (2018) Amazon sailfin catfish Pterygoplichthys pardalis (Loricariidae) in Bangladesh: a critical review of its invasive threat to native and endemic aquatic species. Fishes 3:14. https://doi.org/10.3390/fishes3010014

Islam MS, Hossain MA (1983) An account of the fishes of the Padma near Rajshahi. Rajshahi Fish Bull 1:1–31

Islam SN, Gnauck A (2011) Water salinity investigation in the Sundarbans rivers in Bangladesh. Int J Water 6:74–91

IUCN_Bangladesh (2016) Gharials of Bangladesh. International Union for Conservation of Nature, Bangladesh Country Office, Dhaka, Bangladesh

IUCN_Bangladesh (2015) Red list of Bangladesh: a brief on assessment result 2015. International Union for Conservation of Nature, Bangladesh Country Office, Dhaka, Bangladesh, Bangladesh

IUCN (2020) The IUCN Red List of Threatened Species. Version 2020-2. In: Int. Union Conserv. Nat. Nat. Resour. https://www.iucnredlist.org

Joadder MAR, Galib SM, Haque SMM, Chaki N (2015) Fishes of the river Padma, Bangladesh: current trend and conservation status. J Fish 3:259. https://doi.org/10.17017/jfish.v3i2.2015.111

Jones PE, Tummers JS, Galib SM, et al (2021) The use of barriers to limit the spread of aquatic invasive animal species: a global review. Front Ecol Evol 9:611631. https://doi.org/10.3389/fevo.2021.611631

Ju R, Li X, Jiang J, et al (2020) Emerging risks of non-native species escapes from aquaculture: call for policy improvements in China and other developing countries. J Appl Ecol 57:85–90. https://doi.org/10.1111/1365-2664.13521

Kelkar N, Dey S (2020) Mesh mash: legal fishing nets cause most bycatch mortality of endangered South Asian river dolphins. Biol Conserv 252:108844. https://doi.org/10.1016/j.biocon.2020.108844

Khan MAG, Galib SM, Hasnath M, et al (2022) Exotic fish and decreasing habitats vis-à-vis conservation of freshwater fish biodiversity of Bangladesh. J Fish 10:101301. https://doi.org/10.17017/j.fish.397

Kruskal JB, Wish M (1978) Multidimensional scaling. Sage Publications, London

Kumar D (2017) River Ganges – historical, cultural and socioeconomic attributes. Aquat Ecosyst Health Manag 20:8–20. https://doi.org/10.1080/14634988.2017.1304129

Kuznetsova A, Brockhoff PB, Christensen RHB (2016) lmerTest: Tests in Linear Mixed Effects Models. In: R Packag. version 2.0-33. https://cran.r-project.org/package=lmerTest

Li J, Jin Q, Liang Y, et al (2022) Highly efficient removal of nitrate and phosphate to control eutrophication by the dielectrophoresis-assisted adsorption method. Int J Environ Res Public Health 19:1890. https://doi.org/10.3390/ijerph19031890

Lucas MC, Baras E (2001) Migration of Freshwater Fishes. Blackwell Science, Oxford

MacArthur RH (1957) On the relative abundance of bird species. Proc Natl Acad Sci 43:293–295. https://doi.org/10.1073/pnas.43.3.293

McDonald JH (2014) Handbook of biological statistics, 3rd edn. Sparky House Publishing, Maryland

Mia MY, Hossain MU, Hossain MS, Farzana S (2009) Impact assessment of Farakka barrage on environmental issues at Bheramara Upazila, Bangladesh. Bangladesh J Fish Res 13:89–93

Oksanen J, Guillaume Blanchet F, Friendly M, et al (2018) Vegan: community ecology package. In: R Packag. version 2.4-6. https://cran.r-project.org/package=vegan

Payne AI, Sinha R, Singh HR, Huq S (2004) A review of the Ganges basin: its fish and fisheries. In: Welcomme RL, Petr T (eds) Proceedings of the second international symposium on the management of large rivers for fisheries. Food and Agriculture Organization of the United Nations, Rome, Italy

Pont D, Logez M, Carrel G, et al (2015) Historical change in fish species distribution: shifting reference conditions and global warming effects. Aquat Sci 77:441–453. https://doi.org/10.1007/s00027-014-0386-z

Pörtner HO, Peck MA (2010) Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. J Fish Biol 77:1745–1779. https://doi.org/10.1111/j.1095-8649.2010.02783.x

R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/

Rahman AKA (2005) Freshwater fishes of Bangladesh, 2nd edn. Zoological Society of Bangladesh, Dhaka, Bangladesh

Reid AJ, Carlson AK, Creed IF, et al (2019) Emerging threats and persistent conservation challenges for freshwater biodiversity. Biol Rev 94:849–873. https://doi.org/10.1111/brv.12480

Saha S, Roy K, Roy S, et al (2018) Rooppur nuclear power plant: current status & feasibility. Strojnícky Cas – J Mech Eng 68:167–182. https://doi.org/10.2478/scjme-2018-0033

Sarkar UK, Pathak AK, Sinha RK, et al (2012) Freshwater fish biodiversity in the River Ganga (India): changing pattern, threats and conservation perspectives. Rev Fish Biol Fish 22:251–272. https://doi.org/10.1007/s11160-011-9218-6

Servili A, Canario AVM, Mouchel O, Muñoz-Cueto JA (2020) Climate change impacts on fish reproduction are mediated at multiple levels of the brain-pituitary-gonad axis. Gen Comp Endocrinol 291:113439. https://doi.org/10.1016/j.ygcen.2020.113439

Shahid S (2010) Recent trends in the climate of Bangladesh. Clim Res 42:185–193. https://doi.org/10.3354/cr00889

Shalehin MS, Parvez MT, Lucas MC, Galib SM (2022) A case study of illegal fishing causes during seasonal fishery closure in Kaptai Lake, Bangladesh. Fish Manag Ecol. https://doi.org/10.1111/fme.12536

Strayer DL, Dudgeon D (2010) Freshwater biodiversity conservation: recent progress and future challenges. J North Am Benthol Soc 29:344–358. https://doi.org/10.1899/08-171.1

Sultana N, Islam MN (2016) Fishing gears and methods in the Chalan Beel, Bangladesh. J Fish 4:377. https://doi.org/10.17017/jfish.v4i2.2016.128

Suski CD, Cooke SJ (2007) Conservation of aquatic resources through the use of freshwater protected areas: opportunities and challenges. Biodivers Conserv 16:2015–2029. https://doi.org/10.1007/s10531-006-9060-7

Vörösmarty CJ, McIntyre PB, Gessner MO, et al (2010) Global threats to human water security and river biodiversity. Nature 467:555–561. https://doi.org/10.1038/nature09440

Welcomme RL (1985) River fisheries. Technical paper 262. Food and Organization of the United Nation, Rome, Italy

WII-NMCG (2019) Biodiversity profile of the Ganga River: planning aquatic species restoration for Ganga River. Wildlife Institute of India, Dehradun, Uttarakhand, India

Wilkinson CL, Yeo DCJ, Tan HH, et al (2018) Land-use change is associated with a significant loss of freshwater fish species and functional richness in Sabah, Malaysia. Biol Conserv 222:164–171. https://doi.org/10.1016/j.biocon.2018.04.004

Winemiller KO, McIntyre PB, Castello L, et al (2016) Balancing hydropower and biodiversity in the Amazon,

Congo, and Mekong. Science (80-) 351:128–129. https://doi.org/10.1126/science.aac7082
WWF (2018) Living planet report 2018: aiming higher. WWF International, Gland, Switzerland

Figure captions

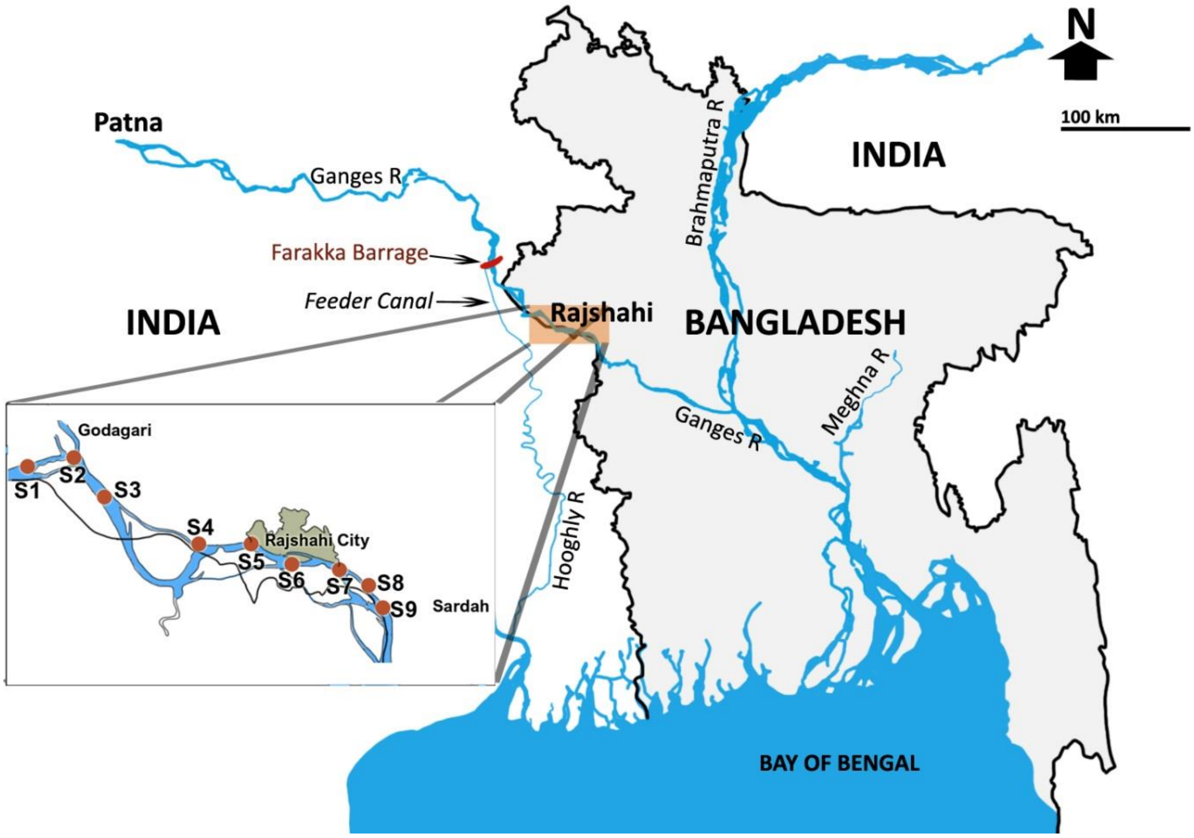

Figure 1: Map of the lower Ganges River in India (from Patna downstream) and Bangladesh showing the fish sampling sites in Rajshahi (inset, S1–S9).

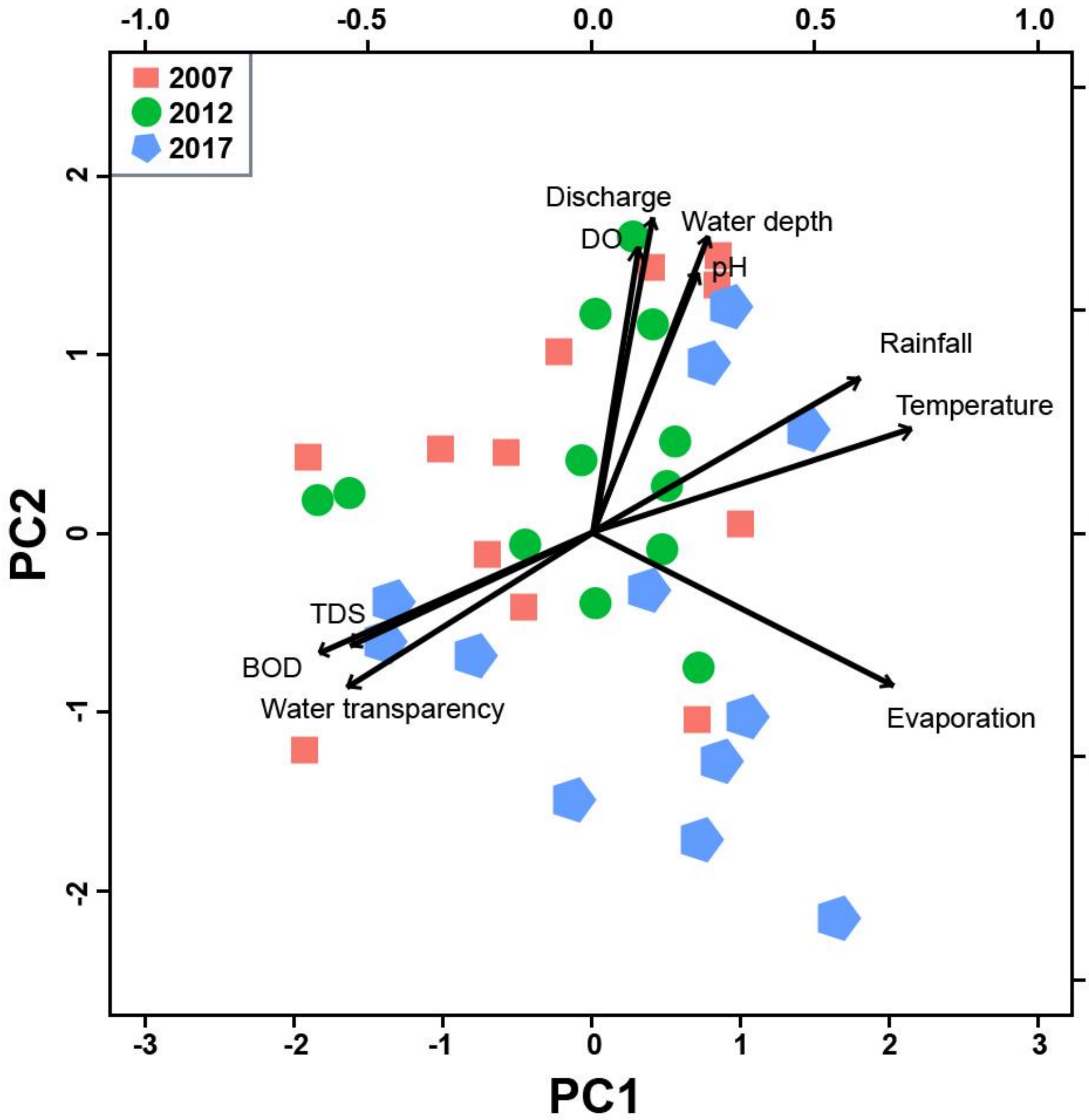

Figure 2: Biplot of principal component analysis of the water quality and environmental parameters. Details of component loadings are given in Table S1. Points represent monthly measurements.

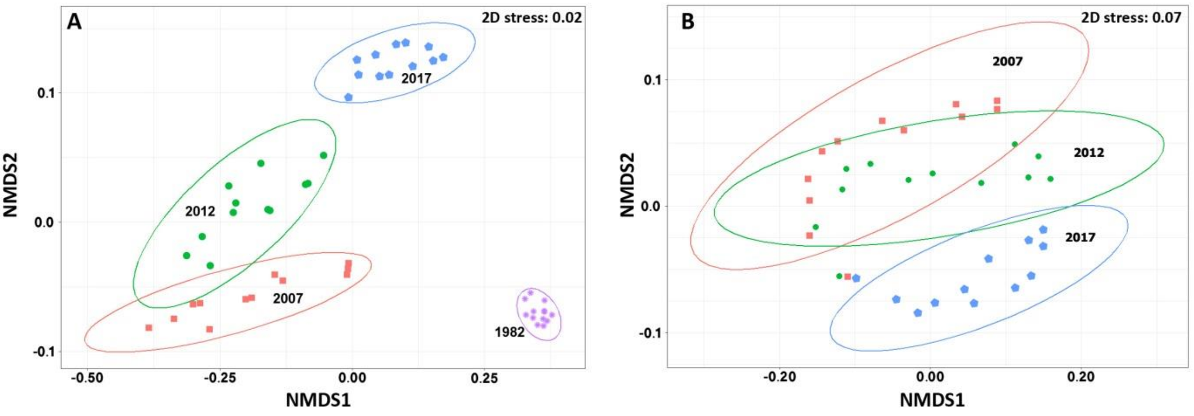

Figure 3: Non-metric Multidimensional Scaling (NMDS) ordination plot showing temporal variations of fish species richness, based on presence-absence data for all four years (A) and abundance data for 2007, 2012 and 2017 (B), in the lower River Ganges, Bangladesh. The ellipses are 95% confidence areas.

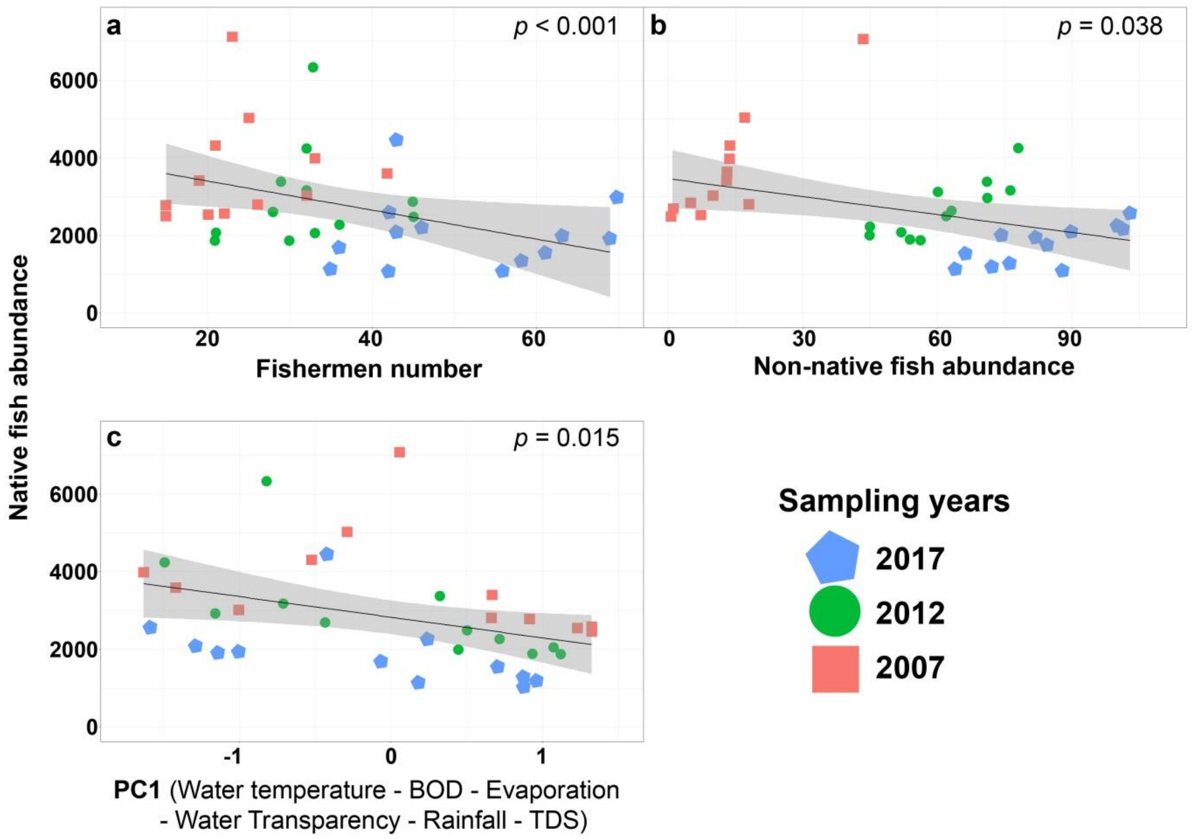

Figure 4: Relationships between native fish abundance and fishing pressure (a), non-native fishes (b) and PC1 (water temperature – BOD – evaporation - water transparency – rainfall - TDS). Grey shaded area represents 95% confidence interval. Data from sampling years are color-coded. Numbers of fishermen are the cumulative totals of those recorded at sample sites each month and represent standardised metrics of fishing pressure; non-native fish abundance is the cumulative total captured across sampled sites per month.

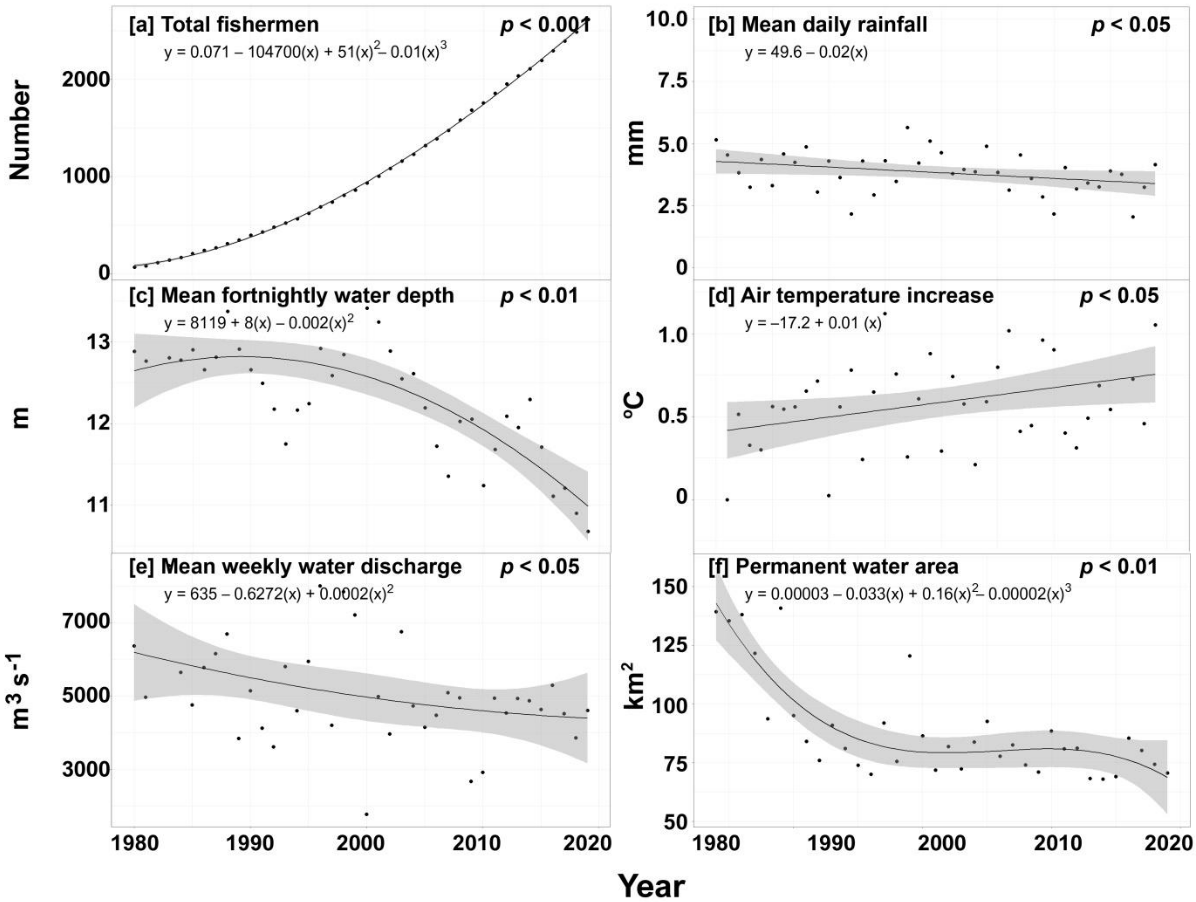

Figure 5: Historical trends of different factors in the study area. Trend line with 95% confidence interval represented by grey-shaded area. Annual numbers of local fishermen is based upon censused numbers from 27 villages adjacent to sampling sites. Increase in air temperature (d) is calculated by treating mean yearly temperature of 1981 as base. Channel depth and discharge of the Ganges at Rajshahi are annual means of fortnightly and weekly measurements respectively; rainfall and air temperature change are annual means of daily measurements, permanent water level was measured from satellite images in the middle of the dry season. Details of the fitted models can be found in Table S2 and validation outputs for model development can be found in Figure S1of the supplementary material.

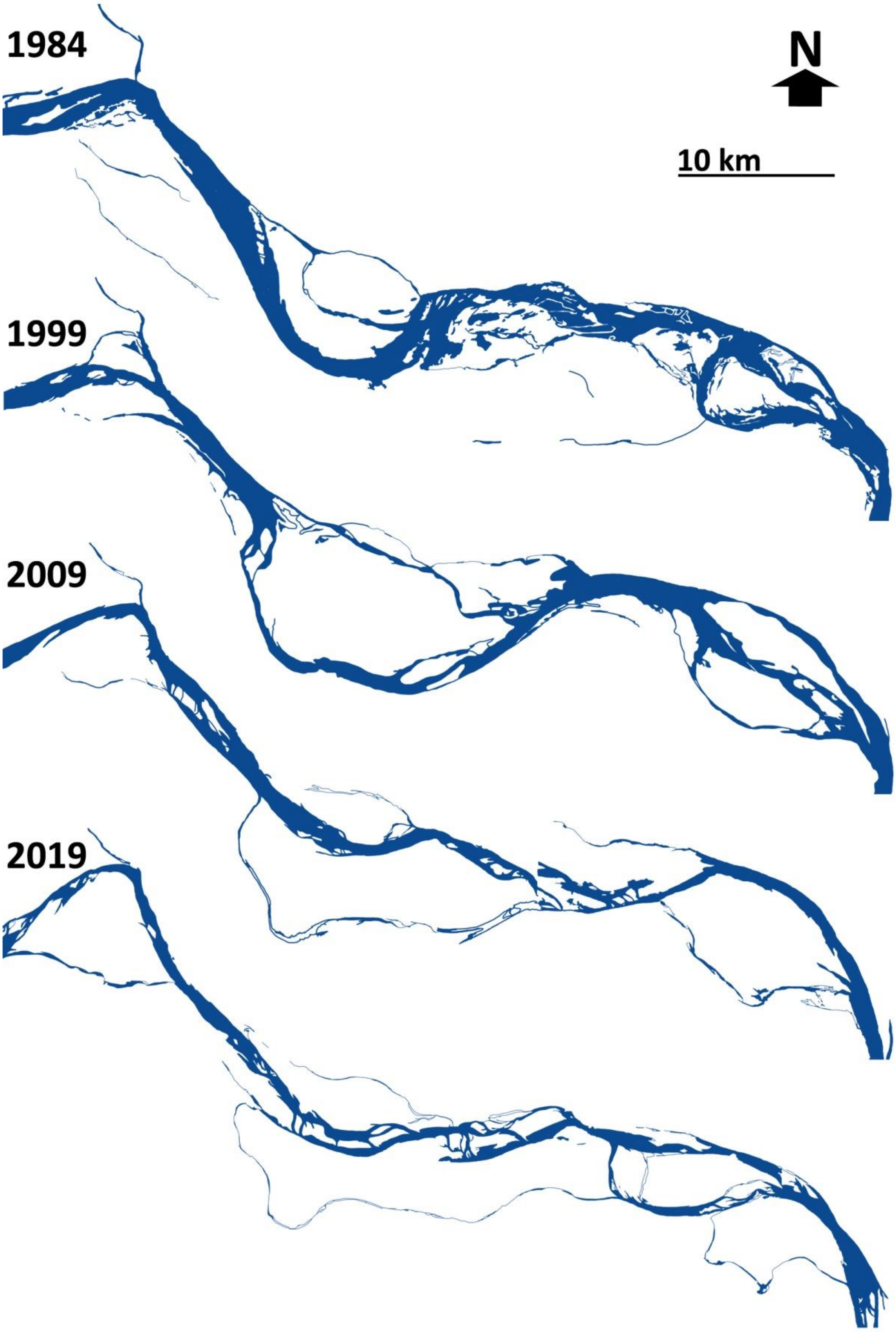

Figure 6: Reduction in permanent water area of the lower River Ganges in the Rajshahi study area (downstream of Farakka Barrage) over time, analysed by QGIS.

Table 1: Summary of the native fish fauna in the lower Ganges River along with important national (Bangladesh) and global conservation status. CR, Critically Endangered; EN, Endangered; NT, Near Threatened; VU, Vulnerable. Detailed species- and sampling year-wise data are presented in Table S2.

Order	**Spp.**	**Conservation status of interest**						**Catch (No.)**		
		National				**Global**		**2007**	**2012**	**2017**
		CR	**EN**	**VU**	**NT**	**VU**	**NT**			
Myliobatiformes	1	–	–	–	–	–	–	42	12	7
Anguilliformes	1	–	–	–	–	–	–	514	478	394
Beloniformes	1	–	–	–	–	–	–	682	585	214
Clupeiformes	6	–	–	1	–	–	–	4341	3438	2399
Cypriniformes	23	–	2	2	5	1	1	13494	10598	5457
Cyprinodontiformes	1	–	–	–	–	–	–	264	209	35
Mugiliformes	1	–	–	–	–	–	–	664	336	201
Osteoglossiformes	2	–	1	1	–	–	1	802	464	258
Perciformes	13	–	1	–	2	–	1	8326	6584	4390
Siluriformes	21	3	5	3	1	1	5	14178	12096	9461
Synbranchiformes	4	–	1	1	1	–	–	844	622	360
Syngnathiformes	2	–	–	1	–	–	–	0	2	0
Tetraodontiformes	1	–	–	–	–	–	–	196	79	14

Table 2: Fish species that were recorded in the lower Ganges study locality in 1982 but absent in the samples of the present study (2007, 2012 and 2017). Names are from Froese and Pauly (2019) whereas national and global conservation status are based on IUCN Bangladesh (2015) and IUCN (2020). CR, Critically Endangered; EN, Endangered; LC, Least Concern; NE, Not Evaluated; NT, Near Threatened; VU, Vulnerable.

Family	**Fish name**	**Conservation status**	
		National	**Global**
Anguillidae	*Anguilla nebulosa*	NE	NT
Hemiramphidae	*Hyporhamphus quoyi*	NE	LC
Pristigasteridae	*Ilisha megaloptera*	LC	LC
Clupeidae	*Gudusia variegata*	NE	LC
	Chela cachius	VU	LC
	Laubuka laubuca	LC	LC
	Securicula gora	NT	LC
	Megarasbora elanga	EN	LC
	Rasbora daniconius	LC	LC
	Puntius stigma	NE	LC
	Oreichthys cosuatis	EN	LC
	Puntius chrysopterus	NE	NE
	Pethia gelius	NT	LC
	Labeo gonius	NT	LC
	Labeo nandina	CR	NT
	Labeo boga	CR	LC
	Labeo pangusia	EN	NT
	Crossocheilus latius	EN	LC
Cobitidae	*Botia dayi*	EN	NE
Mugilidae	*Sicamugil cascasia*	VU	LC
Channidae	*Channa barca*	CR	DD
Ambassidae	*Parambassis baculis*	NT	LC
Sciaenidae	*Otolithes ruber*	NE	LC
Ailiidae	*Proeutropiichthys taakree*	NE	LC
Bagridae	*Hemibagrus menoda*	NT	LC
	Mystus gulio	NT	LC
	Rama rama	NE	NE
Sisoridae	*Gagata gagata*	LC	LC

Table 3: Changes in native fish abundance, richness and community over time in the lower River Ganges, obtained through Linear Mixed-effects Modelling (LMM, for abundance and species richness) and Permutational Multivariate Analysis of Variance (PERMANOVA, for community composition). Bold values indicate outcomes significant at $p \leq 0.05$. Percentage change indicates changes in mean in the latest years.

Comparisons	**LMM and PERMANOVA results**		**Post-hoc test results**			**% change**
	***F*-value**	***p*-value**	**Estimate**	***z*-value**	***p*-value**	
Abundance	592.8	**<0.001**	–	–	–	
2012 vs. 2007	–	–	–0.24	–12.0	**<0.001**	–19.5
2017 vs. 2012	–	–	–44	–33.9	**<0.001**	–34.8
2017 vs. 2007	–	–	–0.68	–22.0	**<0.001**	–47.5
Richness	37.9	**<0.001**	–	–	–	
2012 vs. 2007	–	–	–0.02	–1.3	0.416	–2.9
2017 vs. 2012	–	–	–0.12	–6.8	**<0.001**	–15.6
2017 vs. 2007	–	–	–0.15	–8.1	**<0.001**	–18.1
Community	5.4	**<0.001**	–	–	–	–
2012 vs. 2007	–	**–**	–	–	0.260	–
2017 vs. 2012	–	**–**	–	–	0.126	–
2017 vs. 2007	–	**–**	–	–	**0.038**	–

Table 4: Factors (obtained from Principal Component Analyses) affecting fish fauna in the lower River Ganges during 2007–2017 sampling period, obtained through linear mixed effects modelling (LMM). *p*-values in bold are statistically significant.

Factor	**Estimate**	***F*-value**	***p*-value**
Fishing pressure	–43.6	47.8	**<0.001**
Non-native fishes	–2.3	4.2	**0.038**
PC1	–9.3	7.6	**0.015**
PC2	8.7	2.0	0.173
Non-native fish × PC1	3.4	6.9	**0.019**
Non-native fish × PC2	–3.7	4.1	**0.048**
PC1 × PC2	–8.4	1.4	0.264
Non-native fish × PC1 × PC2	3.8	1.6	0.229

PC1 = Water temperature – BOD – Evaporation – Water Transparency – Rainfall - TDS
PC2 = DO – pH – Water discharge – Water depth

Supplementary information

Fish diversity decline in the lower Gangetic plains: a victim of multiple stressors?

Md. Taskin Parvez, ABM Mohsin, Sadman S. Arnob, Martyn C. Lucas, Nipa Chaki, Md Abdul Gofur Khan, Shams M. Galib

Supplementary tables

Table S1: Component loadings of different water quality and climatic factors affecting fish fauna in the lower Ganges plains, obtained through principal component analysis (PCA). Boldface indicates the highest component loadings for each factor

Factors	PC1	PC2
Water temperature	**0.90**	0.30
Dissolved oxygen	0.13	**0.80**
BOD	**–0.77**	–0.35
Evaporation	**0.85**	–0.43
pH	0.30	**0.73**
Water transparency	**–0.68**	–0.43
Water discharge	0.17	**0.88**
Water depth	0.33	**0.83**
Rainfall	**0.75**	0.43
TDS	**–0.67**	–0.31
Variance explained (%)	39	35
Total variance (%)	74	

Table S2: Regression models used to analyse the relationships between different parameters and time. Model validation output are in Figure S1.

Parameter	Regression type	Equation obtained	Model diagnostic summary			
			Residual SE	R^2	F	p
Fishing pressure	Polynomial	$y = 0.071 – 104700(x) + 51(x)^2 – 0.01(x)^3$	14.3	0.99	38810	<0.001
Rainfall	Simple linear	$y = 49.6 – 0.02(x)$	0.78	0.08	4.54	0.039
Water depth	Polynomial	$y = 8119 + 8(x) – 0.002(x)^2$	0.46	0.61	28.2	<0.001
Temperature	Simple linear	$y = –17.2 + 0.01 (x)$	0.26	0.11	5.45	0.025
Water Discharge	Polynomial	$y = 635 – 0.6272(x) + 0.0002(x)^2$	0.13	0.26	6.8	0.048
Permanent water area	Polynomial	$y = 0.00003 – 0.033(x) + 0.16(x)^2 – 0.00002(x)^3$	0.06	0.64	19.74	<0.001

Table S3: Combined catches (across months and sample sites), standardized by sampling methods, effort and sites, of fish species in different study years in the lower Ganges plains along with their national (BD, Bangladesh) and global (GLO) conservation status. CR, Critically Endangered; DD, Data Deficient; EN, Endangered; LC, Least Concern; NE, Not Evaluated; NN, Non-native in Bangladesh; NT, Near Threatened; VU, Vulnerable.

Order and family	Fish Species	Conservation status		Catch (No.)		
		BD	GLO	2007	2012	2017
Order: Myliobatiformes						
Trygonidae	*Trygon* sp.	NA	NA	42	12	7
Order: Anguilliformes						
Ophichthidae	*Pisodonophis cancrivorus*	LC	NE	514	478	394
Order: Beloniformes						
Belonidae	*Xenentodon cancila*	LC	LC	682	585	214
Order: Clupeiformes						
Clupeidae	*Corica soborna*	LC	LC	978	713	577
	Gudusia chapra	VU	LC	796	553	205
	Gonialosa manmina	LC	LC	234	167	100
	Tenualosa ilisha	LC	LC	761	659	506
Engraulidae	*Setipinna phasa*	LC	LC	778	682	548
	Setipinna taty	LC	LC	794	664	463
Order: Cypriniformes						
Cyprinidae	*Amblypharyngodon mola*	LC	LC	1304	1069	727
	Aspidoparia jaya	LC	LC	651	570	380
	Barbonymus gonionotus	NN	LC	19	132	183
	Cabdio morar	VU	LC	823	625	408
	Cirrhinus cirrhosus	NT	VU	231	140	29
	Cirrhinus reba	NT	LC	458	231	147
	Ctenopharyngodon idella	NN	NE	19	61	133
	Cyprinus carpio	NN	VU	34	185	209
	Esomus danrica	LC	LC	1373	1017	708
	Gibelion catla	LC	LC	208	111	16
	Hypophthalmichthys molitrix	NN	NT	27	291	309
	Hypophthalmichthys nobilis	NN	DD	44	119	171
	Labeo calbasu	LC	LC	138	115	22
	Labeo bata	LC	LC	903	711	584
	Labeo rohita	LC	LC	172	167	71
	Osteobrama cotio	NT	LC	1017	847	647
	Pethia conchonius	LC	LC	133	102	26
	Pethia phutunio	LC	LC	58	40	32
	Pethia ticto	VU	LC	147	143	17
	Puntius chola	LC	LC	294	187	154
	Puntius sophore	LC	LC	1642	1543	945
	Salmostoma bacaila	LC	LC	421	351	19
	Salmostoma phulo	NT	LC	432	388	105
	Systomus sarana	NT	LC	1543	1333	67
Botiidae	*Botia dario*	EN	LC	401	188	109
Cobitidae	*Botia lohachata*	EN	NE	263	98	15
	Lepidocephalichthys guntea	LC	LC	629	490	219
Nemacheilidae	*Acanthocobitis botia*	LC	LC	253	132	10
Order: Cyprinodontiformes						
Aplocheilidae	*Aplocheilus panchax*	LC	LC	264	209	35
Order: Mugiliformes						
Mugilidae	*Rhinomugil corsula*	LC	LC	336	201	127
Order: Osteoglossiformes						
Notopteridae	*Chitala chitala*	EN	NT	192	113	23
	Notopterus notopterus	VU	LC	272	145	57
Order: Perciformes						
Anabantidae	*Anabas testudineus*	LC	LC	364	238	61

Order and family	Fish Species	Conservation status		Catch (No.)		
		BD	GLO	2007	2012	2017
Ambassidae	*Parambassis lala*	LC	NT	49	20	1
	Parambassis ranga	LC	LC	861	428	104
	Chanda nama	LC	LC	2220	1903	1576
Channidae	*Channa marulius*	EN	LC	257	157	62
	Channa punctata	LC	LC	737	634	488
	Channa striata	LC	LC	248	194	90
Cichlidae	*Oreochromis niloticus*	NN	LC	14	22	39
Badidae	*Badis badis*	NT	LC	213	81	0
Osphronemidae	*Trichogaster fasciata*	LC	LC	360	269	164
	Trichogaster lalius	LC	LC	290	129	28
Nandidae	*Nandus nandus*	NT	LC	234	144	11
Gobiidae	*Glossogobius giuris*	LC	LC	1770	1571	1178
Sciaenidae	*Otolithoides pama*	LC	DD	723	816	627
Order: Siluriformes						
Bagridae	*Mystus cavasius*	NT	LC	289	225	85
	Mystus tengara	LC	LC	1114	965	825
	Mystus vittatus	LC	LC	328	284	0
	Sperata aor	VU	LC	145	83	13
	Sperata seenghala	VU	LC	333	319	210
	Rita rita	EN	LC	918	775	606
Clariidae	*Clarias batrachus*	LC	LC	199	146	19
	Clarias gariepinus	NN	LC	0	0	12
Heteropneustidae	*Heteropneustes fossilis*	LC	LC	193	125	15
Loricariidae	*Pterygoplichthys disjunctivus*	NN	NE	0	0	8
Pangasiidae	*Pangasius pangasius*	EN	LC	317	129	36
Schilbeidae	*Ailia coila*	LC	NT	2397	2262	2176
	Clupisoma garua	EN	LC	581	511	471
	Eutropiichthys murius	LC	LC	164	108	47
	Eutropiichthys vacha	LC	LC	1722	1567	1064
	Pachypterus atherinoides	LC	LC	2033	1875	1715
Siluridae	*Ompok bimaculatus*	EN	NT	398	250	152
	Ompok pabo	CR	NT	0	0	15
	Ompok pabda	EN	NT	303	142	113
	Wallago attu	VU	VU	301	203	107
Sisoridae	*Bagarius bagarius*	CR	NT	176	56	14
	Gagata cenia	LC	LC	2267	2071	1777
	Sisor rabdophorus	CR	LC	0	0	1
Order: Synbranchiformes						
Mastacembelidae	*Mastacembelus armatus*	EN	LC	356	305	230
	Macrognathus aculeatus	NT	NE	165	144	71
	Macrognathus pancalus	LC	LC	228	127	33
Synbranchidae	*Monopterus cuchia*	VU	LC	95	46	26
Order: Tetraodontiformes						
Tetraodontidae	*Leiodon cutcutia*	LC	LC	117	79	14
	Chelonodon patoca	DD	LC	79	0	0
Order: Syngnathiformes						
Syngnathidae	*Microphis cuncalus*	VU	LC	0	2	0

Table S4: Similarity percentage analysis (SIMPER), based on Bray-Curtis dissimilarity index on abundance data of fishes in lower Ganges River, Bangladesh (2007 and 2012).

Fish species	Ratio (average / SD)	Average		*p*-values	Contribution (%)
		2007	2012		
Tenualosa ilisha	1.11	5.17	4.76	0.993	4.51
Gagata cenia	1.36	13.23	12.69	0.978	2.73
Ailia coila	1.27	13.67	13.24	1	2.60
Puntius sophore	1.30	11.31	10.64	0.871	2.57
Chanda nama	1.38	13.30	12.05	0.401	2.56
Hypophthalmichthys molitrix[a]	3.29	1.30	4.88	**0.001**	2.55
Esomus danrica	1.34	10.38	8.68	0.134	2.32
Pachypterus atherinoides	1.32	12.63	12.12	0.945	2.28
Systomus sarana	1.36	11.11	10.05	0.362	2.15
Eutropiichthys vacha	1.38	11.71	11.05	0.873	2.08
Amblypharyngodon mola	1.49	10.26	9.10	0.114	1.84
Parambassis ranga	2.42	8.41	5.90	**0.001**	1.80
Cyprinus carpio[a]	2.05	1.39	3.87	**0.001**	1.79
Chelonodon patoca	3.74	2.44	0.00	**0.001**	1.69
Glossogobius giuris	1.55	12.09	11.22	0.131	1.63
Otolithoides pama	1.42	7.65	7.86	0.697	1.59
Barbonymus gonionotus[a]	2.24	1.04	3.23	**0.001**	1.55
Osteobrama cotio	1.48	9.08	8.15	0.168	1.54
Labeo bata	1.44	8.54	7.46	0.184	1.48
Corica soborna	1.27	8.87	7.51	0.173	1.48
Setipinna phasa	1.34	7.82	7.28	0.95	1.48
Cirrhinus reba	1.62	6.04	4.21	**0.002**	1.47
Cirrhinus cirrhosus	1.30	4.19	2.92	0.113	1.41
Botia lohachata	1.77	4.63	2.70	**0.001**	1.38
Clarias.batrachus	1.49	3.95	2.99	0.09	1.33
Botia.dario	1.58	5.68	3.87	**0.001**	1.32
Pangasius pangasius	1.73	5.02	3.23	**0.001**	1.27
Gudusia chapra	1.24	8.00	6.68	**0.029**	1.23
Bagarius bagarius	2.25	3.80	2.08	**0.001**	1.22
Heteropneustes fossilis	1.55	3.87	2.87	0.073	1.21
Labeo calbasu	1.39	3.08	2.70	0.799	1.20
Rita rita	1.46	8.60	7.94	0.282	1.19
Cabdio morar	1.37	8.20	7.08	**0.046**	1.19
Mystus tengara	1.33	9.54	8.81	0.17	1.18
Lepidocephalus guntea	1.18	7.17	6.21	0.22	1.13
Badis badis	2.29	4.17	2.55	**0.001**	1.13
Trichogaster lalius	2.57	4.88	3.26	**0.001**	1.11
Notopterus notopterus	1.93	4.72	3.35	**0.002**	1.10
Gibelion catla	1.44	4.04	2.82	**0.014**	1.10
Ompok pabda	1.96	4.97	3.41	**0.001**	1.08
Clupisoma garua	1.42	6.87	6.38	0.738	1.05
Hypophthalmichthys nobilis[a]	1.54	1.72	3.03	**0.002**	1.04
Pisodonophis cancrivorus	1.45	6.45	6.15	0.776	1.04

Fish species	Ratio (average / SD)	Average		*p*-values	Contribution (%)
		2007	**2012**		
Aspidoparia jaya	1.33	7.27	6.74	0.5	1.03
Xenentodon cancila	1.46	7.42	6.89	0.389	1.02
Salmostoma phulo	1.44	5.91	5.52	0.611	1.00
Ompok bimaculatus	1.36	5.60	4.50	**0.02**	0.99
Salmostoma bacaila	1.24	5.84	5.23	0.565	0.99
Acanthocobitis botia	1.52	4.54	3.23	**0.001**	0.98
Macrognathus pancalus	1.19	4.30	3.08	**0.005**	0.97
Chitala chitala	1.18	3.87	2.86	**0.047**	0.96
Gonialosa manmina	1.46	4.34	3.54	0.17	0.94
Anabas testudineus	1.58	5.44	4.36	**0.003**	0.94
Sperata aor	1.43	3.44	2.41	**0.004**	0.93
Rhinomugil corsula	1.45	5.22	4.03	**0.002**	0.92
Puntius chola	1.44	4.84	3.86	**0.020**	0.92
Setipinna taty	1.39	8.07	7.36	0.132	0.91
Mastacembelus armatus	1.46	5.36	4.91	0.344	0.87
Sperata seenghala	1.18	5.10	5.09	0.736	0.87
Monopterus cuchia	1.24	2.76	1.72	**0.005**	0.86
Eutropiichthys murius	1.42	3.57	2.85	0.124	0.84
Parambassis lala	1.48	1.91	0.93	**0.009**	0.84
Wallago attu	1.59	4.95	4.03	**0.006**	0.84
Nandus nandus	1.73	4.36	3.39	**0.002**	0.82
Channa punctata	1.40	7.78	7.22	0.284	0.80
Ctenopharyngodon idella[a]	1.23	1.09	2.05	**0.019**	0.78
Channa marulius	1.66	4.58	3.59	**0.001**	0.74
Mystus cavasius	1.56	4.84	4.27	0.091	0.73
Pethia ticto	1.50	3.45	3.28	0.375	0.71
Aplocheilus panchax	1.42	4.63	4.09	0.193	0.71
Trygon sp.	1.35	1.78	0.85	**0.001**	0.69
Trichogaster fasciata	1.55	5.43	4.69	**0.029**	0.69
Mystus vittatus	1.40	5.16	4.80	0.787	0.68
Labeo rohita	1.27	3.65	3.69	0.377	0.64
Leiodon cutcutia	1.37	3.08	2.51	**0.032**	0.54
Channa striata	1.52	4.52	3.99	**0.020**	0.48
Macrognathus aculeatus	1.45	3.68	3.40	0.288	0.47
Pethia phutunio	1.20	2.09	1.77	0.381	0.45
Pethia conchonius	1.45	3.31	2.89	**0.038**	0.41
Oreochromis niloticus[a]	0.97	0.96	1.32	0.053	0.35
Microphis cuncalus	0.30	0.00	0.12	0.952	0.09

a, non-native species. Bold values indicate outcomes significant at $p \leq 0.05$.

Table S5: Similarity percentage analysis (SIMPER), based on Bray-Curtis dissimilarity index on abundance data of fishes in lower Ganges River, Bangladesh (2007 and 2017).

Fish species	**Ratio (average / SD)**	**Average**		***p*-values**	**Contribution (%)**
		2007	**2017**		
Systomus sarana	3.51	11.11	1.44	**0.001**	4.06
Tenualosa ilisha	1.07	5.17	3.87	0.999	2.63
Parambassis ranga	4.09	8.41	2.74	**0.001**	2.38
Mystus vittatus	8.42	5.16	0.00	**0.001**	2.15
Salmostoma bacaila	4.15	5.84	0.85	**0.001**	2.08
Ailia coila	1.46	13.67	12.71	1	1.90
Chanda nama	1.35	13.30	10.71	0.484	1.86
Badis badis	9.81	4.17	0.00	**0.001**	1.75
Acanthocobitis botia	3.70	4.54	0.49	**0.001**	1.72
Gudusia chapra	2.25	8.00	3.88	**0.001**	1.69
Gagata cenia	1.40	13.23	11.68	0.978	1.69
Pangasius pangasius	2.39	5.02	1.18	**0.001**	1.63
Glossogobius giuris	1.45	12.09	9.39	**0.049**	1.58
Hypophthalmichthys molitrix[a]	3.32	1.30	5.03	**0.001**	1.58
Botia lohachata	3.96	4.63	0.87	**0.001**	1.58
Puntius sophore	1.27	11.31	8.43	0.064	1.56
Xenentodon cancila	1.92	7.42	3.88	**0.001**	1.55
Lepidocephalus guntea	1.67	7.17	3.74	**0.001**	1.53
Nandus nandus	4.51	4.36	0.76	**0.001**	1.50
Esomus danrica	1.36	10.38	7.32	**0.008**	1.49
Trichogaster lalius	3.97	4.88	1.36	**0.001**	1.47
Eutropiichthys vacha	1.35	11.71	9.04	0.07	1.47
Pachypterus atherinoides	1.36	12.63	11.50	1	1.47
Amblypharyngodon mola	1.43	10.26	7.36	**0.005**	1.46
Aplocheilus panchax	2.49	4.63	1.25	**0.001**	1.45
Salmostoma phulo	1.88	5.91	2.51	**0.001**	1.45
Anabas testudineus	2.67	5.44	1.97	**0.001**	1.43
Cirrhinus cirrhosus	2.26	4.19	0.97	**0.001**	1.38
Cirrhinus reba	1.74	6.04	3.06	**0.001**	1.33
Gibelion catla	2.95	4.04	0.82	**0.001**	1.33
Setipinna phasa	1.07	7.82	5.97	0.994	1.29
Botia dario	1.92	5.68	2.74	**0.001**	1.25
Rita rita	1.17	8.60	6.56	0.403	1.25
Bagarius bagarius.	3.39	3.80	0.87	**0.001**	1.24
Mystus cavasius	1.62	4.84	2.05	**0.001**	1.24
Heteropneustes fossilis	2.58	3.87	0.94	**0.001**	1.22
Clarias batrachus	2.59	3.95	1.04	**0.001**	1.21
Barbonymus gonionotus[a]	2.84	1.04	3.86	**0.001**	1.20
Cyprinus carpio[a]	2.24	1.39	4.13	**0.001**	1.18
Sperata aor	2.94	3.44	0.66	**0.001**	1.18
Macrognathus pancalus	3.07	4.30	1.51	**0.001**	1.17
Wallago attu	1.56	4.95	2.42	**0.002**	1.16
Notopterus notopterus	2.56	4.72	2.02	**0.001**	1.15

Fish species	Ratio (average / SD)	Average		*p*-values	Contribution (%)
		2007	2017		
Corica soborna	1.46	8.87	6.70	**0.034**	1.10
Cabdio morar	1.86	8.20	5.71	**0.001**	1.09
Labeo bata	1.20	8.54	6.61	0.2	1.08
Chitala chitala	2.64	3.87	1.28	**0.001**	1.08
Channa marulius	2.17	4.58	2.07	**0.001**	1.06
Pethia ticto	2.65	3.45	1.00	**0.001**	1.04
Rhinomugil corsula	1.42	5.22	2.88	**0.002**	1.02
Chelonodon patoca	3.84	2.44	0.00	**0.001**	1.01
Mystus tengara	1.13	9.54	7.94	0.612	1.00
Leiodon cutcutia	2.61	3.08	0.76	**0.001**	0.96
Osteobrama cotio	1.46	9.08	7.19	**0.014**	0.95
Ompok bimaculatus	1.62	5.60	3.44	**0.001**	0.93
Ctenopharyngodon idella	2.48	1.09	3.27	**0.001**	0.93
Clupisoma garua	1.43	6.87	5.88	0.976	0.92
Setipinna taty	2.02	8.07	6.11	**0.001**	0.91
Channa punctata	1.52	7.78	6.12	0.097	0.91
Channa striata	1.59	4.52	2.42	**0.002**	0.91
Eutropiichthys murius	1.52	3.57	1.54	**0.002**	0.89
Otolithoides pama	1.38	7.65	6.90	0.999	0.88
Labeo calbasu	1.58	3.08	1.07	**0.002**	0.88
Hypophthalmichthys nobilis[a]	1.95	1.72	3.71	**0.001**	0.86
Pethia conchonius	2.55	3.31	1.26	**0.001**	0.85
Mastacembelus armatus	1.29	5.36	4.01	0.219	0.82
Pisodonophis cancrivorus	1.50	6.45	5.42	0.343	0.82
Trichogaster fasciata	1.83	5.43	3.58	**0.001**	0.80
Aspidoparia jaya	1.50	7.27	5.54	**0.002**	0.79
Labeo rohita	1.45	3.65	2.09	**0.018**	0.79
Ompok pabda	2.76	4.97	3.05	**0.001**	0.78
Parambassis lala	2.94	1.91	0.08	**0.001**	0.75
Puntius chola	1.48	4.84	3.37	**0.015**	0.75
Monopterus cuchia	1.73	2.76	1.16	**0.001**	0.72
Sperata seenghala	1.53	5.10	4.13	**0.007**	0.64
Gonialosa manmina	1.61	4.34	2.84	**0.001**	0.64
Macrognathus aculeatus	1.84	3.68	2.33	**0.001**	0.58
Trygon sp.	1.66	1.78	0.53	**0.001**	0.52
Oreochromis niloticus[a]	1.04	0.96	1.49	0.966	0.40
Pethia phutunio	1.22	2.09	1.49	0.311	0.36
Clarias gariepinus[a]	0.66	0.00	0.55	0.398	0.25
Ompok pabo	0.76	0.00	0.65	0.255	0.25
Pterygoplichthys disjunctivus[a]	0.56	0.00	0.40	0.974	0.16
Sisor rabdophorus	0.30	0.00	0.08	1	0.03

a, non-native species. Bold values indicate outcomes significant at $p \leq 0.05$.

Table S6: Similarity percentage analysis (SIMPER), based on Bray-Curtis dissimilarity index on abundance data of fishes in lower Ganges River, Bangladesh (2012 and 2017).

Fish species	Ratio (average / SD)	Average		*p*-values	Contribution (%)
		2012	2017		
Systomus sarana	2.66	10.05	1.44	**0.001**	4.74
Tenualosa ilisha	1.06	4.76	3.87	0.999	3.33
Mystus vittatus	6.42	4.80	0.00	**0.001**	2.67
Ailia coila	1.48	13.24	12.71	1	2.49
Salmostoma bacaila	2.96	5.23	0.85	**0.001**	2.40
Chanda nama	1.32	12.05	10.71	1	2.34
Puntius sophore	1.24	10.64	8.43	0.333	2.08
Gagata cenia	1.39	12.69	11.68	1	2.07
Glossogobius giuris	1.18	11.22	9.39	0.359	2.01
Eutropiichthys vacha	1.40	11.05	9.04	0.225	1.90
Pachypterus atherinoides	1.34	12.12	11.50	1	1.84
Xenentodon cancila	1.82	6.89	3.88	**0.003**	1.79
Parambassis ranga	2.27	5.90	2.74	**0.001**	1.76
Salmostoma phulo	1.67	5.52	2.51	**0.001**	1.72
Esomus danrica	1.37	8.68	7.32	0.627	1.70
Setipinna phasa	1.14	7.28	5.97	0.992	1.69
Lepidocephalus guntea	1.48	6.21	3.74	**0.006**	1.67
Amblypharyngodon mola	1.29	9.10	7.36	0.38	1.67
Aplocheilus panchax	2.26	4.09	1.25	**0.001**	1.63
Gudusia chapra	1.75	6.68	3.88	**0.001**	1.57
Otolithoides pama	1.52	7.86	6.90	0.431	1.56
Acanthocobitis botia	2.72	3.23	0.49	**0.001**	1.54
Nandus nandus	3.21	3.39	0.76	**0.001**	1.44
Rita rita	1.12	7.94	6.56	0.68	1.44
Badis badis	4.52	2.55	0.00	**0.001**	1.42
Mystus cavasius	1.47	4.27	2.05	**0.001**	1.37
Labeo bata	1.28	7.46	6.61	1	1.32
Anabas testudineus	1.80	4.36	1.97	**0.001**	1.30
Cirrhinus cirrhosus	1.62	2.92	0.97	**0.013**	1.30
Mystus tengara	1.23	8.81	7.94	1	1.29
Pethia ticto	1.85	3.28	1.00	**0.001**	1.27
Pangasius pangasius.	1.86	3.23	1.18	**0.001**	1.26
Clupisoma garua.	1.39	6.38	5.88	0.998	1.22
Corica soborna.	1.35	7.51	6.70	0.698	1.22
Clarias batrachus	1.44	2.99	1.04	**0.004**	1.17
Wallago attu	1.39	4.03	2.42	**0.016**	1.16
Osteobrama cotio	1.43	8.15	7.19	0.501	1.16
Gibelion catla	1.82	2.82	0.82	**0.001**	1.11
Labeo calbasu	1.73	2.70	1.07	**0.006**	1.10
Channa punctata	1.60	7.22	6.12	0.137	1.09
Pisodonophis cancrivorus	1.45	6.15	5.42	0.856	1.08
Trichogaster lalius	2.34	3.26	1.36	**0.001**	1.07
Heteropneustes fossilis	1.42	2.87	0.94	**0.001**	1.06

Fish species	Ratio (average / SD)	Average		p-values	Contribution (%)
		2012	2017		
Cirrhinus reba	1.42	4.21	3.06	0.083	1.05
Mastacembelus armatus	1.37	4.91	4.01	0.45	1.05
Botia lohachata	1.83	2.70	0.87	**0.001**	1.04
Cabdio morar	1.48	7.08	5.71	**0.025**	1.01
Sperata aor	1.74	2.41	0.66	**0.001**	1.00
Labeo rohita	1.42	3.69	2.09	**0.003**	1.00
Channa striata	1.39	3.99	2.42	**0.003**	0.97
Leiodon cutcutia	1.96	2.51	0.76	**0.001**	0.96
Macrognathus pancalus	1.80	3.08	1.51	**0.001**	0.95
Chitala chitala	1.56	2.86	1.28	**0.001**	0.94
Eutropiichthys murius	1.41	2.85	1.54	**0.042**	0.91
Rhinomugil corsula	1.20	4.03	2.88	0.125	0.90
Pethia conchonius	2.03	2.89	1.26	**0.001**	0.90
Aspidoparia jaya	1.34	6.74	5.54	0.062	0.89
Channa marulius	1.55	3.59	2.07	**0.001**	0.88
Setipinna taty	1.63	7.36	6.11	**0.005**	0.88
Botia dario	1.32	3.87	2.74	**0.043**	0.83
Notopterus notopterus	1.53	3.35	2.02	**0.002**	0.81
Ctenopharyngodon idella[a]	1.61	2.05	3.27	**0.002**	0.80
Trichogaster fasciata	1.46	4.69	3.58	**0.007**	0.75
Bagarius bagarius	1.51	2.08	0.87	**0.001**	0.70
Ompok bimaculatus	1.35	4.50	3.44	**0.001**	0.70
Puntius chola	1.46	3.86	3.37	0.6	0.68
Sperata seenghala	1.41	5.09	4.13	**0.01**	0.67
Gonialosa manmina	1.28	3.54	2.84	**0.035**	0.66
Macrognathus aculeatus	1.57	3.40	2.33	**0.006**	0.65
Monopterus cuchia	1.48	1.72	1.16	0.21	0.65
Hypophthalmichthys nobilis[a]	1.32	3.03	3.71	0.069	0.58
Barbonymus gonionotus[a]	1.41	3.23	3.86	**0.02**	0.51
Parambassis lala	1.11	0.93	0.08	**0.008**	0.49
Oreochromis niloticus[a]	1.06	1.32	1.49	0.992	0.46
Hypophthalmichthys molitrix[a]	1.23	4.88	5.03	1	0.38
Pethia phutunio	1.22	1.77	1.49	0.95	0.38
Cyprinus carpio[a]	1.35	3.87	4.13	0.388	0.37
Trygon sp.	1.13	0.85	0.53	0.404	0.34
Clarias gariepinus[a]	0.65	0.00	0.55	0.124	0.34
Ompok pabo	0.76	0.00	0.65	0.083	0.33
Ompok pabda	1.44	3.41	3.05	0.188	0.29
Pterygoplichthys disjunctivus[a]	0.56	0.00	0.40	0.304	0.22
Microphis cuncalus	0.30	0.12	0.00	**0.002**	0.08
Sisor rabdophorus	0.30	0.00	0.08	1	0.04

a, non-native species. Bold values indicate outcomes significant at $p \leq 0.05$.

Supplementary figures

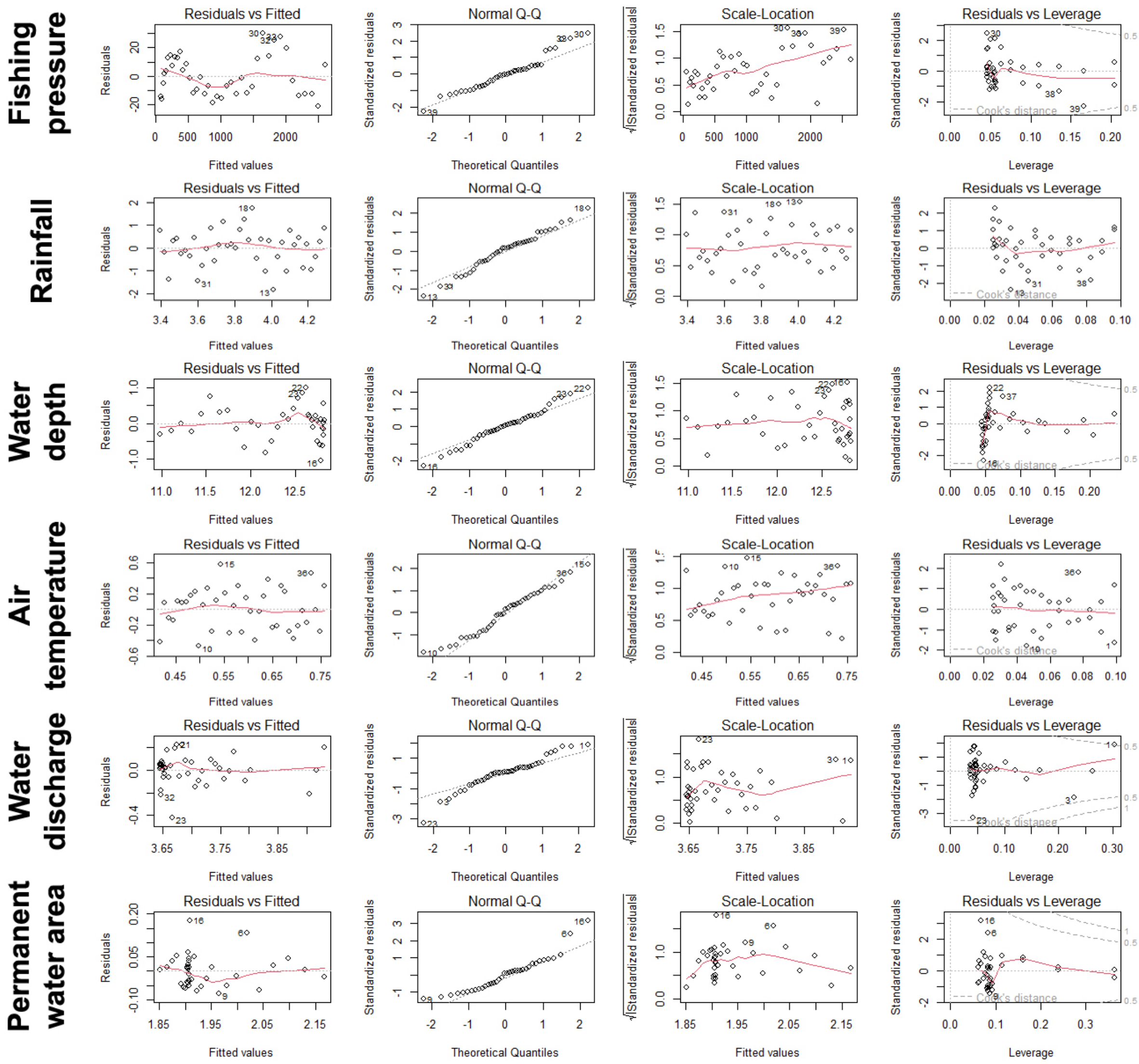

Figure S1: Regression model validation outputs, used to determine changes in habitat and environmental changes in the lower Ganges over time. Outputs are based on polynomial models for fishing pressure, water depth, water discharge and permanent water area and simple linear regression models for rainfall and air temperature.

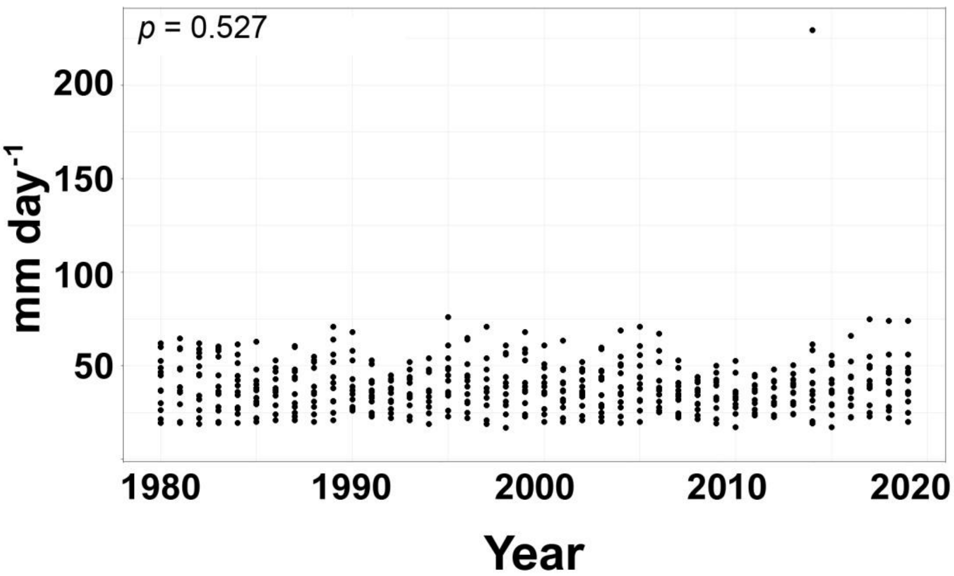

Figure S2: Historical data of evaporation rate in the lower Ganges study area (downstream of Farakka Barrage), showing no significant trend.

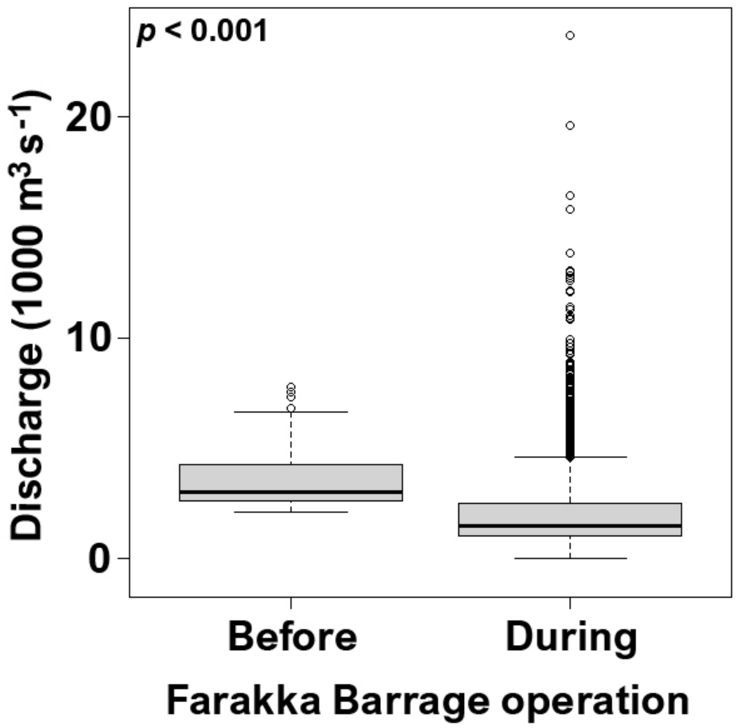

Figure S3: Boxplot of weekly measurements of water discharge in the Ganges downstream of Farakka Barrage during the dry season (November–March) before (1969–1974) and during (1975–2017) Farakka Barrage operation. Midline within the box is the median; upper and lower limits of the box represent the third and first quartiles (75th and 25th percentiles) respectively.

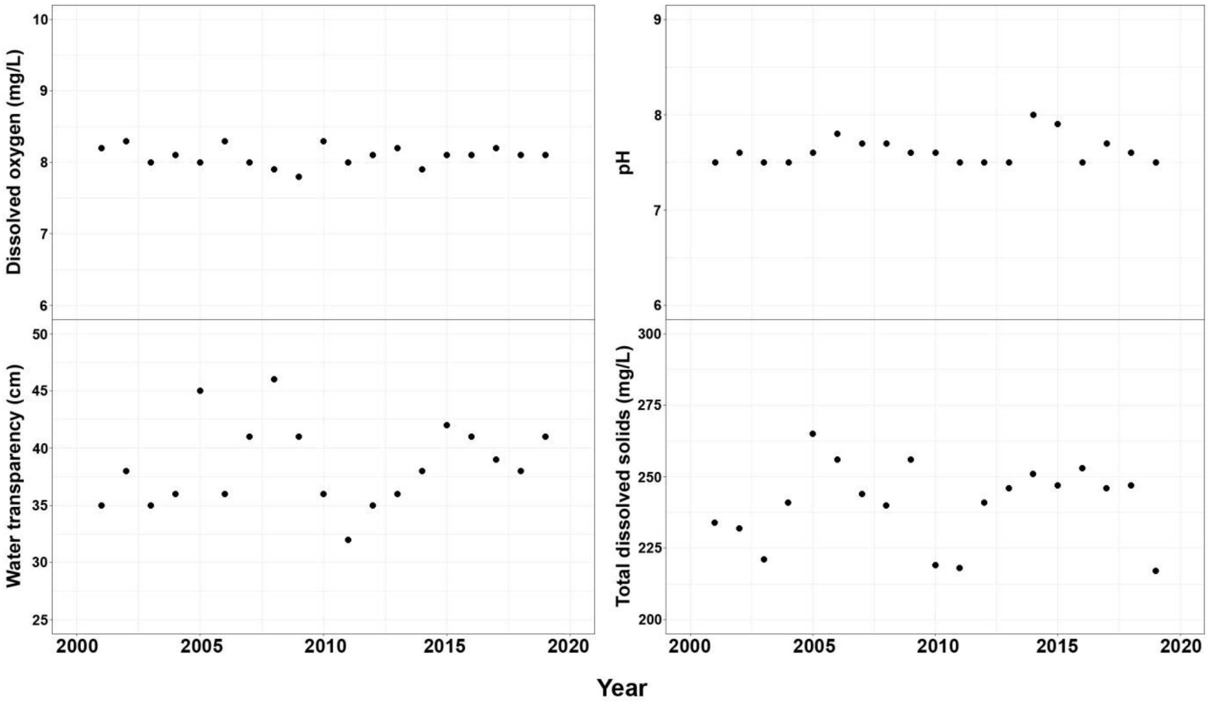

Figure S4: Mean dissolved oxygen, pH, water transparency and total dissolved solids at the Boalia point of the lower Ganges between 2001 and 2019. Data were collected in three seasons, summer, monsoon and winter every year.

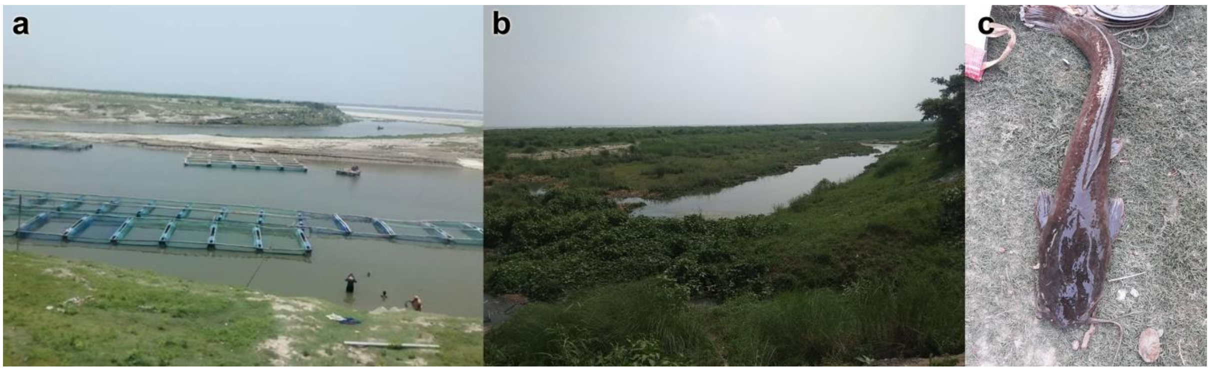

Figure S5: Aquaculture of non-native fishes in the lower Ganges, Bangladesh; (a) cage culture, (b) pen culture in an isolated waterbody during the dry season, and (c) an escaped predatory African sharptooth catfish *Clarias gariepinus*, weighing 3.7 kg, caught in a fisherman's net from the main Ganges channel.