Invasive vermiculated sailfin catfish (*Pterygoplichthys disjunctivus*) has an impact on highly valued native fish species

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SG, ML and ABM designed the study. MTP, MIH, NC and SG carried out fieldwork and laboratory analysis. SG and NC analysed the data and drafted the manuscript; ML and JS participated in data analysis and critically revised the manuscript; SG coordinated the study. All authors gave final approval for publication.

Conflict of interest

We declare we have no competing interests.

Data availability statement

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

ABSTRACT

Invasion by armoured catfishes (Loricariidae) is a threat to native fish communities of warm, freshwater habitats. Following importation as an ornamental species, the vermiculated sailfin catfish *Pterygoplichthys disjunctivus*, has become established in inland waters of Bangladesh. We recorded the distribution of sailfin catfish in Bangladesh. Vermiculated sailfin catfish was recorded in 17 rivers across the majority of the country, with well-established breeding populations in four localities. We measured competition between three native carps and sailfin catfish by determining growth and survival, and by carrying out gut analysis. The competition experiment was carried out using a randomised block design in earthen ponds with similar physico-chemical parameters to freshwater habitats in Bangladesh. It demonstrated that growth and survival rate of native cyprinid fishes can be adversely impacted in the presence of sailfin catfish. In high-density catfish treatments, growth of *Cirrhinus cirrhosus* (bottom-feeding omnivore), *Labeo rohita* (midwater omnivore) and *Catla catla* (pelagic planktivore) was reduced by 48.4%, 21.4% and 2.4% respectively, compared to controls containing the three cyprinids but no catfish. Survival of *C. cirrhosus* reduced to 70% in high-density catfish treatments, compared to 100% in catfish-free ponds, with lesser effects on the other species. Low- and medium-density catfish treatments generated lesser growth and survival effects. Catfish diet remained stable across density treatments, but diet of native fishes deviated increasingly from control values as catfish density increased. This study demonstrates impacts of sailfin catfish on native fish species and the increasing distribution of sailfin catfish in Bangladesh.

Keywords: Non-native species; armoured catfish; competition; invasive species; conservation

1 | INTRODUCTION

Globally, species richness in terrestrial and aquatic ecosystems is falling rapidly due to both anthropogenic and natural causes (Naeem et al. 2012). The current species extinction rate exceeds the likely background extinction rate by about a factor of one thousand (Pimm et al. 2014). Among the various reasons for declining biodiversity worldwide, biological invasion of non-native species is playing a key role (Lodge 1993; Naeem et al. 2012; Caffrey et al. 2014). The impact of non-native aquatic species can be severe, by altering ecosystems, leading to the decline or extinction of native species, and having major economic outcomes such as affecting fisheries and habitat integrity (Manchester and Bullock 2000; García-Berthou et al. 2005; Galib et al. 2022). Biological invasions may alter trophic relationships through reductions in community species richness, potentially resulting in altered predator - prey relationships (Gherardi et al. 2009; Galiana et al. 2014; Hempel et al. 2016). Colonisation by invasive species is one of the most important threats to biodiversity at a global scale (Sala et al. 2000; Mora and Sale 2011) and, in most parts of the world, is considered to be the single most important threat to freshwater biodiversity and ecological function (Lodge et al. 2000). Modified waterbodies are potentially more susceptible to invasive species (Moyle 1976; Marchetti et al. 2004), primarily because of their links to human activities including intentional or accidental introduction of non-native species by humans (Chapple et al. 2012) and the presence of exotic species can be used as an indicator of degraded conditions (Kennard et al. 2005).

Although not all non-native species become invasive (Williamson 1989), they can impact native biodiversity directly or indirectly (Silva et al. 2009). Established non-native species can frequently outcompete native species in terms of environmental tolerance (Marchetti et al. 2004; Canonico et al. 2005), breeding success (Pompei et al. 2016), predation (Brown and Moyle 1991; McDowall 2006), resource acquisition and body size (Lowery and Holdich 1988; Mack et al. 2000; Bubb et al. 2006). However, there are similarly examples of non-native species that have minimal apparent impacts on native biota (Thomas and Palmer 2015). Transmission of disease agents by non-native species (e.g. crayfish plague by signal crayfish *Pacifastacus leniusculus*, rosette agent by topmouth gudgeon *Pseudorasbora parva*, and tapeworms by grass carp *Ctenopharyngodon idella*) can wipe out entire populations of native species (Harlioğlu and Harlioğlu 2006) or cause chronic declines (Gozlan et al. 2005) including endangered species (Moyle 1993). A diverse range of aquatic biota may be affected by the introduction of non-natives (Chen 1989; Caffrey et al. 2014), and could result in serious population decline or extinction of natives (Vitule et al. 2009; Galib et al. 2021).

Biological invasion threats by non-natives demand appropriate management strategies requiring knowledge of factors such as distribution, likely routes of spread, and likely ecological consequences of the spread of non-native species (Britton et al. 2011). For freshwater fishes those strategies and the underpinning knowledge are, however, still not well developed (Britton et al. 2010) and are entirely absent in many developing countries. Despite legislation being in place to control non-natives and their introduction in many countries, non-native fishes are continuously released locally to support fisheries and aquaculture practices (e.g. food aquaculture, ornamental fish and sport fishing; Gozlan 2008), and this is increasingly common as a means for supplementing fisheries in developing countries (Copp et al. 2005; Vitule et al. 2009). Efforts are therefore needed in those areas that have both a high conservation value and a high risk of non-native species introduction to limit the losses of global aquatic biodiversity (Gozlan et al. 2010). Many developing countries support rich biological resources and are also susceptible to biological invasion through human activities associated with development (Copp et al. 2007; Dawson et al. 2017). Despite the considerable attention that invasive species receive, little data on the ecological impacts of invasive fishes are available in many regions including South Asia, and thus their effects on native populations, communities and ecosystems are largely unknown (Parker et al. 1999; Simberloff 2006). Most studies on non-native species distribution and ecology have been carried out in temperate regions of the globe, with little or limited information in large parts of Asia and Africa (García-Berthou 2007; Dawson et al. 2017). Bangladesh, a sub-tropical country located in South Asia, supports rich aquatic biodiversity (e.g. >265 freshwater fish species; Rahman 2005) where a large number of non-native fishes (>90) were also introduced for aquarium trade and aquaculture (Galib and Mohsin 2011).

Sailfin catfishes, potentially comprising several species within the genus *Pterygoplichthys* (Loricariidae) were imported to Bangladesh in 1980 as ornamental fish species (Rahman 2005). The species has been misidentified (as *Hypostomus plecostomus*) in the country for a long time (Hossain et al. 2018). The dorsal fin and ventro-lateral surface marks confirm that the species available in water bodies of Bangladesh (Figure S1) is vermiculated sailfin catfish *Pterygoplichthys disjunctivus* (see Page and Robins 2006 and Hoover et al. 2014). This species is a facultative air-breathing, benthic omnivorous species with strong colonisation capabilities (Hoover et al. 2014). This species has been reported from at least six countries outside of its native range (India, China, Philippines, Mexico, Thailand and USA) (Chaichana et al. 2011; Wei et al. 2017; CABI 2019), but little information is available concerning its impact on native species and ecosystems (Gibbs et al. 2013; Hoover et al. 2014). Increasing concern has been expressed for the spread and potential impacts of this and closely related species on the Indian subcontinent (Galib and Mohsin 2010; Hussan et al. 2016; Hossain et al. 2018; Das et al. 2020; Raj et al. 2020).

In Bangladesh, frequent catches in inland waters (e.g. rivers, ponds, lake etc.) and strong colonisation capabilities of vermiculated sailfin catfish have been observed over the last two decades (Galib and Mohsin 2010; Chaki et al. 2014; Galib 2015) but systematic records of such data is lacking. In Bangladesh, as in much of South East Asia, biological invasion is a risk to native biodiversity but has not received the attention it requires (Peh 2010; Galib et al. 2018). It is essential to assess the level of risk posed by the presence of non-native species in the environment for effective management (Britton et al. 2011). With increasing numbers of reports of sailfin catfish in Bangladesh in almost all types of inland water bodies over the past few years, there is a concern for its potential impacts on native species. In this study, mesocosm trials using earthen ponds were carried out, to determine whether sailfin catfish of varying densities affect growth and survival of high-value native fish species. This study also meets one of the proposals by Hoover et al. (2014) who emphasised controlled experiments investigating impacts of sailfin catfish. We hypothesised that effects would be greater on native species with a similar benthic-feeding niche to sailfin catfish, than on species feeding higher in the water column. In addition, we also compiled distribution data of sailfin catfish for the first time in the country.

2 MATERIALS AND METHODS

Two aspects of sailfin catfish ecology were examined in this study. First, the distribution of sailfin catfish in aquatic habitats of Bangladesh was determined through a combination of field survey, literature searching, personal and social media communications. Second, a mesocosm study in earthen ponds was conducted to evaluate the impacts of vermiculated sailfin catfish on growth and survival of high-valued native fish species, recorded to be co-occurred with sailfin catfish in most of the habitats in the country.

2.1 Distribution of sailfin catfish in aquatic habitats of Bangladesh

For depicting the distribution scenario for sailfin catfish in Bangladesh, a combination of personal and social media communication and literature searches were made, together with limited field survey calibration. For data from social media, we asked for sailfin catfish records with proof (photo or video) to members of various Bangladesh-based popular Facebook groups or pages related to ornamental fish or fisheries of Bangladesh. We noted associated details (date and location of sailfin catfish catch, number and approximate sizes of individuals, habitat, impact note, source, purpose of introduction etc.) for each occurrence record.

During literature searching, we searched Web of Science, Scopus and Google Scholar databases for records of sailfin catfish occurrence in aquatic habitats of Bangladesh. The following key words were used: Amazon sailfin catfish OR sailfin catfish OR suckermouth catfish AND Bangladesh. In addition, key words were also used in Google search, in both English and Bangla, to find relevant grey literature and newspaper articles. Results were subjected to manual checking to select the appropriate studies for further consideration, from which species, site location, habitat type, date, introduction and impact or other important notes were extracted (see Table S1 for details). We also asked 45 fishermen on the Buriganga River, central Bangladesh, to provide an estimate of sailfin catfish contribution to their total catch. To validate their estimation, we employed cast net (4.8 m^2) sampling in March–April 2022 (n = 31 times, between 1000 and 1400 hours) in the Buriganga River and analysed the catch. Fishermen in the Buriganga River were also asked to reveal post-harvest distribution of sailfin catfish.

2.2 Mesocosm study

This study was carried out in earthen ponds situated in Baraigram Upazila (sub-district) of Natore district, Northwest Bangladesh for a period of eight months from April to November 2019. A four month long (September to December) pilot experiment with similar research design without any replication of the current treatments (except biomass control for natives) was also carried out in 2016 in the field laboratory of the Department of Fisheries in the University of Rajshahi, Bangladesh.

Experimental ponds: The experiment was carried out in 2019, in twenty earthen fish farm ponds of similar size (25 m^2 each) and characteristics. These non-flowing ponds represent conditions that are common in lentic floodplain habitats across Bangladesh. Ponds were distributed in an elongated array of 10 ponds × 2 ponds with ~1 m distance between each of the ponds. All the ponds were well-exposed to natural daylight (~8 hours of sunlight per day). The ponds were dried completely by dewatering two months before the stocking of fishes. All the pond embankments were fenced by mosquito nets to exclude predators (snakes, frogs etc.) from entering. Nets were also used 1 m above the water surface to cover the ponds to prevent water-bird predation. Water from adjacent non-experimental ponds was supplied into the experimental ponds 1.5 months before stocking of fishes. Ponds were primarily rain-fed, but additional water was supplied through a deep-tubewell (groundwater pump) when needed to maintain the desired water depth (1 m).

Collection of fishes: Vermiculated sailfin catfish were procured from local aquarium shops. Native fish species for use in the experiments were selected based on their co-occurrence with sailfin catfish in most of the habitats in the country, recorded through the distribution study described earlier, their regional importance and feeding niches. Three indigenous carp species (*Catla catla*, *Labeo rohita* and *Cirrhinus cirrhosus*) were used. Feeding niches of all these species are well-known – top layer planktivore (*C. catla*), mid-water omnivore (*L. rohita*) and bottom-feeding omnivore (*C. cirrhosus*) (Yadav 1997). All these indigenous species are highly valued for aquaculture in Bangladesh. Moreover, *C. cirrhosus* is also of conservation importance and ranked as 'Near Threatened' in Bangladesh (IUCN_Bangladesh 2015) and 'Vulnerable' globally (Rema Devi and Ali. A. 2011). Fingerlings of these three carp species were collected from local fish nursery operators. Care was taken during selection of individuals of fishes for the study to ensure good health and size similarity of all the individuals.

Study design: A randomized block design method with three treatments ($T_1 – T_3$; with varying densities of sailfin catfish) and two controls (C_1, without sailfin catfish; C_2, biomass control for natives), each with four replicates ($R_1 – R_4$), was employed to measure the impact of sailfin catfish on native fish species. The number of native fish individuals was the same in each treatment and first control (T_1 – T_3 and C_1; five *L. rohita*, five *C. catla* and five *C. cirrhosus*). The numbers of sailfin catfish in different experimental groups were zero (in C_1 and C_2), five (in T_1), 10 (in T_2) and 15 (in T_3). Mean (± SD, range) stocking weights of different species were: sailfin catfish, 8.4 ± 0.2 g (8.2 – 8.9 g); *C. catla*, 9.2 ± 0.2 g (8.9 – 9.6 g); *L. rohita*, 9.1 ± 0.3 g (8.7 – 9.5 g); and *C. cirrhosus*, 8.9 ± 0.2 g (8.6 – 9.4 g). In C_2, densities of natives were adjusted (i.e. nine *L. rohita*, ten *C. catla* and ten *C. cirrhosus*) to make it similar to the total biomass of natives and sailfin catfish in high density treatment (T_3) to test for any biomass effect. The densities of native carps were similar to those in native environments of Bangladesh and also common in aquaculture ponds (T. Pervez, unpublished data). For, sailfin catfish, experimental densities covered a range observed in several ponds and in the Buriganga River in Bangladesh (S. Galib and T. Parvez; personal observation), in the absence of wider information on densities of sailfin catfish in their non-native range (Hoover et al. 2014). The experimental design with mesocosms is a common and well-established method in assessing the potential competitive impact of a particular animal species on the target species, including for fishes (Greig et al. 2013; Tran et al. 2015; Galib et al. 2022).

No extrinsic food was supplied to the ponds. Bamboo branches (five in each pond; ~1.3 m long [1 – 1.2 cm diameter] with six–eight sub-branches [30 – 40 cm long], cut, dead and placed vertically in the water, pushed into the bed) were provided in each pond to facilitate natural food production (e.g. periphyton). Growth of fishes, in terms of weight gain, was monitored monthly through random sampling of at least 60% of the total number of each species. A seine net (mesh 7×7 mm) was used to catch the fishes for sampling and fishes were returned unharmed after weighing. At the end of the experiment each pond was drained (26–27 November 2019) and all fish were counted, weighed and measured. From these raw data, the survival rate and growth rate of each species in each pond were calculated.

Water quality parameters: Physico-chemical parameters (water temperature, water transparency, dissolved oxygen, ammonia and pH) were measured weekly at each pond, normally in the morning, when oxygen levels would be near to daily minimum values. Water temperatures and dissolved oxygen (DO) levels were measured with a digital DO meter (model DO-5510, Lutron electronic). Water transparency was measured by using a Secchi Disc. pH and concentration of ammonia nitrogen (NH_3-N; mg L^{-1}) were measured using a digital HANNA pH meter (model HI 8424) and ammonia medium range photometer (model HI96715) respectively.

2.3 Gut content analysis

At the end of the experiment, native fishes and sailfin catfish were killed by pithing; the gastrointestinal tract was removed through dissection and the gut (stomach and first intestinal loop; Pound et al. 2011) contents were dispensed into labelled vials. A volumetric method through displacement, a reliable method for herbivorous and mud-feeding fishes, was employed to quantify the gut contents after dissecting the gut out of the fish (Hynes 1950). Gut contents were placed on a tray with 100 × 100 mm grid bottom and examined under the microscope (Novel Biological Microscope XSZ-107, China) and the extent of each transect covered by a particular food category was recorded and used to transform into a percentage to remove the varying gut volume (Clements and Choat 1993). A proportion of sailfin catfish (60, n = 5 from each pond) and native fish species (15 *C. catla*, 15 *L. rohita*, 15 *C. cirrhosus*; n = 3 from each pond) was studied for gut contents. In addition to sailfin catfish from experimental ponds, we also examined gut contents of 42 wild *P. disjunctivus* (216.1–268.7 mm), to compare the findings between experimental and wild habitats. Wild sailfin catfish were collected from a fully-established population in the Buriganga River (23°42'36.6"N 90°23'42.5"E), Bangladesh, where the river is degraded due to water pollution (Khan et al. 2022).

2.4 Data analysis

The statistical software R (version 3.3.1; R Core Team 2022) was used to analyse the data, employing an α level of significance of 0.05. Linear Mixed-Effects Models (LMMs) were employed to analyse repeated measures fish growth data using the 'lme4' and 'lmerTest' packages (Bates et al. 2015; Kuznetsova et al. 2016) in R. LMMs were also used to compare various physico-chemical parameters among different treatments. During all these statistical tests, treatments were considered a fixed effect whereas sampling time (i.e. months) and replications were considered random effects. The gut content proportion data were averaged per study pond to avoid pseudoreplication from within the ponds (Bondar et al. 2005). LMMs were also employed to analyse gut content data in which treatments were used as the fixed effect and replications were used as the random effect. The multcomp package (Hothorn et al. 2008) was used for post-hoc analysis. Data were checked for normality by Shapiro-Wilk test (Peat and Barton 2005) and transformed on a log (x+1) scale to meet the statistical test assumption before the test (Clarke 1993).

3 RESULTS

3.1 Distribution of sailfin catfish

Sailfin catfish have been recorded from at least 17 rivers in Bangladesh, of which well-established populations, through natural breeding, were recorded in four rivers (Buriganga, Turag, Sitalakkha and Atrai) (Figure 1, Table S1). All specimens, whose identification was possible by examining specimens or photographs, were identified as vermiculated sailfin catfish (*Pterygoplichthys disjunctivus*). Although the occurrence of sailfin catfish in the

Atrai River was first reported in 2014, it took less than five years for the Buriganga, Turag and Shitalakshya rivers to transition from the first record to full establishment of the population (earliest occurrence report was in 2017 in the Buriganga). In the Buriganga River catchment, more than 98% of the reports of sailfish catfish occurrence in ponds, mostly of large individuals, have been confirmed in at least five districts with no known introduction record (Figure 1, Table S1). Sailfin catfish breeding nests were observed in several ponds of the Pirojpur district in southern Bangladesh. Among other habitats, in addition to local floodplains (locally known as "beels") sailfin catfish have also been recorded in Kaptai Lake, a large impoundment with a major fishery for native species in the southeast region (Figure 1). A well-established population in Gulshan Lake, in the capital city, Dhaka, was also recorded (Figure 1, Table S1).

All respondent fishermen ($n = 45$) confirmed that sailfin catfish in the Buriganga River comprised more than 98% of the total catch, except for during the rainy season (June–August) when contribution of sailfin catfish decreased a little, to 90% of the total catch. Our sampling data in March–April agrees with the fishermen's estimation as 100% of our catch was sailfin catfish. The catch per unit effort ($n = 31$, mean ± SD) was 19.9 ± 5.9 (range 8 – 33) individuals per cast net, indicating a relatively dense minimum population density of 4.1 ± 1.2 individuals m^{-2} (range: 1.7 – 6.9 individuals m^{-2}).

3.2 Mesocosm study

3.2.1 Impact on growth of native species

Despite no significant difference in growth of the three native carps between the two control groups (all $p > 0.05$; Tables 1 & S2 their growth declined with increasing density of sailfin catfish (Tables 1 & S2; Figure 2). Growth of carps in the high-density sailfin catfish treatment decreased by 2.4% for *C. catla*, 21.4% for *L. rohita* and 48.4% for *C. cirrhosus* compared to controls with no sailfin catfish. A significant, yet minor, growth reduction for *C. catla* was only evident at the highest sailfin catfish density (Table S2), but for *L. rohita* and *C. cirrhosis* growth reduction occurred across all densities of sailfin catfish (Figure 2; Table S2). Despite changes in density, sailfin catfish growth (mean final body mass varied from 46.95 g [in T_1] – 47.43 g [in T_2]) did not vary across treatment groups (LMM: $F = 2.2$, $p = 0.122$) (Table 1).

3.2.2 Survival of fishes

No mortality of any species occurred in ponds containing the two control groups (C_1 and C_2). Only one individual of *C. cirrhosus* (zero mortality for other species) died in the low-density sailfin catfish treatment. The survival rate of sailfin catfish was very high (>98–100%) in all treatments. For native species in the medium-density catfish treatment, the survival rate was 95%, 95% and 85% for *C. catla*, *L. rohita* and *C. cirrhosus* respectively (expressed as percentage of total stocked per treatment, from combined replicates). However, in the high-density catfish treatment, the survival rate was much lower for *C. cirrhosus* (70%) than for *C. catla* and *L. rohita* (90% each). Survival rate of *C. cirrhosus* differed significantly between control groups (both C_1 and C_2) and the high density treatment of sailfin catfish (Tables 1 & S2). Survival rate of *C. cirrhosus* also differed between low / medium and high sailfin catfish density treatments (all $p < 0.001$; Tables 1 & S2).

3.2.3 Physico-chemical parameters in mesocosm study

Mean (± SD) water temperature varied seasonally from a minimum of 22.9 ± 0.9 ºC (T_3 in November) to a maximum of 31.6 ± 0.6 ºC (T_2 in June) but did not vary significantly among treatments ($F = 0.83$, $p = 0.48$). Minimum DO was 4.5 mg L^{-1}, recorded in August but no variation was recorded among groups ($p > 0.05$). Other water quality parameters (water transparency, pH and NH_3-N) also did not vary significantly among the treatments over the study period.

3.3 Gut content analysis

A total of six categories of gut contents including algae (mainly periphyton), macrophyte fragments, zooplankton (primarily cladocerans, ostracods and copepods), macroinvertebrates, organic detritus (unrecognisable plant fragments) and mud (fine inorganic-dominated particulate matter) were recorded (Figure 3). For the three native species, all food contents differed significantly across experimental groups (Table 2). In *C. catla*, ingestion of algae, macrophytes and detritus increased whereas zooplankton and macroinvertebrates decreased in experimental groups with sailfin catfish (i.e. $T_1 – T_3$; Figure 3, Tables 2 & S3). For *L. rohita* and *C. cirrhosus*, intake of mud content increased, whereas other food contents mostly decreased in treatment groups with sailfin catfish (Figure 3, Tables 2 & S4–S5).

For sailfin catfish, none of the diet categories differed significantly across treatment groups except macroinvertebrates, for which intake decreased significantly (LMM: $F = 10.2$, $p = 0.005$) with increasing sailfin catfish density (Figure 3; Tables 2 & S6). For wild sailfin catfish, gut contents were dominated by mud (54.4 ± 8.3%, 40 – 70%) and organic detritus (40.1 ± 6.3%, 30 – 51%) (Figure 4).

4 DISCUSSION

This study provides evidence of impacts of sailfin catfish on several native species of aquaculture and conservation importance under controlled mesocosm conditions, as well as the first distribution records in Bangladesh. Growth rate of each of the native species, but especially *C. cirrhosus* and *L. rohita*, was increasingly reduced at greater densities of sailfin catfish. This suggests that sailfin catfish has the capability to affect native species in freshwater habitats in Bangladesh in which sailfin catfish occurrence, including sexually mature individuals, is now common. This species is believed to have been introduced to inland waters of Bangladesh by aquarists (aquarium hobbyists) in the country. In Bangladesh, aquarists often release ornamental fishes into nearby water bodies when individuals outgrow tanks (Galib and Mohsin 2010), underlining potential effects of the industry on both native aquatic species and the environment. However, introduction as a result of the aquarium trade is also a common mode of non-native fish introduction worldwide and loricariid catfishes are no exception to this trend (Hoover et al. 2014).

The sailfin catfish has been recorded in the main river systems (Padma-Meghna-Jamuna/Brahmaputra) of Bangladesh, which poses a tremendous threat to native aquatic biota (Parvez et al. 2022). Well-established populations through natural breeding have been recorded in the Buriganga, Turag, Shitalakshya and Atrai rivers, of which the first three are heavily degraded systems due to discharge of industrial effluents, where dissolved oxygen levels can fall to zero (Khan et al. 2022). Capabilities of tolerating semi-saline water (6–12 ppt) and hypoxic conditions, the latter as a result of air-breathing, using accessory respiratory organs (Capps et al. 2011; Hoover et al. 2014) reflect this species' high environmental tolerance. Rapid expansion of sailfin catfish populations in heavily polluted rivers also supports the pattern that degraded habitats, subjected to human interference, are more vulnerable to non-native species (Kennard et al. 2005; Dawson et al. 2017).

Successful breeding following introduction has also been recorded in aquaculture ponds in Bangladesh. The mean fecundity of *P. disjunctivus* is quite high in invaded ecosystems, ranging from 3655 to 6902 (Gibbs et al. 2008). This species exhibits a high degree of parental care (Hoover et al. 2014) that increases the survival rate of offspring, whereas all the highly fecund species in Bangladesh waters do not offer any parental care to their offspring. This suggests the potential for rapid colonisation and dominance over native species if sailfin catfish escape into the wild. After establishment, loricariid catfish can decrease the fishery production of target species (Mendoza-Alfaro et al. 2009; Hossain et al. 2018). In eight lakes of central Florida, loricariid catfishes became common or dominant (forming up to 80% of total commercial fish catch) within a decade of first being noticed (1990s – 2000s), during which time catches of native (catfish and game fish) and non-native (tilapias) target fishery species declined to as low as 20% of total catch (Mendoza-Alfaro et al. 2009). Commercial fishing became non-profitable and ceased at half of these lakes. The lifespan of loricariid catfishes in the wild is up to about 8 years while it may reach 20 years in aquaria (Hoover et al. 2014), both of which are much higher than the majority of the native freshwater fish species of Bangladesh.

Although the feeding niche of *C. catla* (pelagic planktivore) is different from sailfin catfish (bottom feeder) this study suggests they can still be affected when sailfin catfish density is high in the environment. Although *P. disjunctivus* is primarily a bottom feeder, as found in the wild population studied here, invading loricariids may disperse throughout the receptor habitat, exploiting foods from everywhere, suggesting the potential for widespread interference effects (Nico et al. 2009; Gibbs et al. 2013). Strong impacts were evident for the midwater omnivore *L. rohita*, but the greatest effects on growth and mortality were evident for the bottom-feeding omnivore *C. cirrhosis*, as hypothesised. The low growth of sailfin catfish in this study is, perhaps, surprising but no growth data for sailfish catfish alone were gathered in this study against which to gauge interspecific effects. However, sailfin catfish can grow at 10 cm year^{-1} and, considering the early stage of life, similar growth to our study may be expected (Gibbs et al. 2013). No change in sailfin catfish growth across treatments of varying density indicates that they can maintain similar growth under high density conditions. For sailfin catfish, similar growth rates to those in this study have been observed in many aquaculture ponds in north western Bangladesh (T. Pervez and S. Galib; unpublished data). Sailfin catfish is naturally much slower-growing than the native species used in this study, likely explaining the observed difference in growth. In Bangladesh the maximum reported sizes of *C. catla*, *L. rohita* and *C. cirrhosus* are 96.7 cm (19.8 kg), 94 cm (12.5 kg) and 84 cm (8.8 kg) respectively (Rahman, 2005) whereas, *P. disjunctivus* can grow to a maximum size of approximately 70 cm in its non-native range (Fuller et al. 1999), though ultimate body size in Florida was 52 cm (Gibbs et al. 2013). Growth rate of native species in two control treatments (with no sailfin catfish) was broadly similar to the expected growth rate in ponds where no artificial feed is provided (Rahman, 2010) but it was much lower in other treatments for *L. rohita* and *C. cirrhosus*. The growth of *P. disjunctivus* was lower (~by 20 – 30%) in our study ponds than the growth rate reported in other occupied habitats outside the native range (Gibbs et al. 2013). This may be due to differences in habitats where the current data were collected from smaller ponds whereas the referenced data were based on a river in the US. However, in Bangladeshi rivers, fast growth of *P. disjunctivus* has been reported by professional fishermen, noted during the sampling for the current study (e.g. in Buriganga River) and individuals up to 2.5 kg (~65 cm)were reported to be common in the river.

The survival rate of *C. cirrhosus* was relatively low compared to the other two native cyprinid species when the density of sailfin catfish was high. This suggests that *C. cirrhosus*, a species of conservation importance (IUCN Bangladesh, 2015), can be strongly impacted by the presence of this non-native catfish species. This might be owing to the overlapping trophic niche as large populations of loricariid catfish have been found to compete directly with native fishes in the US and may be disrupting trophic relationships and nutrient cycling (Pound et al. 2011; Hoover et al. 2014).

The sailfin catfish feeds primarily on algae, macrophytes, detritus, sand/mud and to a lesser extent crustaceans, insects, molluscs, fish eggs and other similar organisms (Gestring et al. 2010), also reflected in the gut content analysis in this study. There was strong dietary overlap with *C. cirrhosus* and *L. rohita*, but much less so with the pelagic planktivore *C. catla*. Many other native freshwater fish species in Bangladesh in the silty rivers and floodplains of Bangladesh are omnivores (Yadav 1997; Rahman 2005). Thus, strong competition for the same foods might be expected when this non-native is in a waterbody with other native species, both in Bangladesh and more widely. Not only fishes, but populations of other algae-feeding species (e.g. snails) may also be impacted by loricariid catfishes (Howells 2005; Hoover et al. 2014). However, dietary similarities between native and non-natives do not necessarily equate to high levels of competition because of the typically high abundance of the main food resource of sailfin catfish (algae or detritus of algal origin) (Gestring et al. 2010). Nevertheless, loricariids can strongly impact aquatic ecosystems by decreasing periphyton biomass, altering periphyton nutrient ratios, facilitating detrital decomposition; changing invertebrate community composition, and altering benthic habitat (Scott et al. 2012; Capps and Flecker 2013; Hoover et al. 2014). The long-term presence of loricariid catfish in their native habitats can influence nutrient cycling by disproportionately retaining key nutrients (Hood et al. 2005; Zimmer et al. 2006; Higgins et al. 2006). Rates and ratios by which nutrients are recycled by fishes are a function of body nutrient composition (i.e. stoichiometry) and nutrient composition of their food (Schindler and Eby 1997; Vanni et al. 2002). Bodies of armoured loricariids are rich in phosphorus which results in high retention and low excretion of the nutrients in the waterbody (Vanni et al. 2002; Hood et al. 2005). This may result in reduced availability of key nutrients such as phosphorus for other fishes and is a potential mechanism by which growth in *C. cirrhosus* and *L. rohita* was strongly inhibited.

A peculiar habit of *P. disjunctivus* sucking the body surface of other fishes was observed in aquaria (S. Galib and I. Hossain; personal observation) as well as during trial experiments. This might disrupt the natural immunity of other species as protective mucus on the skin may be damaged and make fish more prone to parasites or pathogens. For example they may be more susceptible to the ectoparasitic copepod *Argulus* which often causes heavy mortality of carp species in freshwater habitats of Bangladesh (Rahman, 2005). However, no obvious disease outbreaks were evident in our study. Alternatively, under wild conditions, the low susceptibility of loricariid catfishes to predators due to their armour plating and large spines might cause these populations to be a trophic 'dead end' in the food web in receiving ecosystems (Pound et al. 2011).

In this study, physico-chemical parameters did not vary between mesocosm pond treatments, and so had no influence on measured growth and mortality of the study species. Conversely, increased sailfin catfish density had no impact on the measured water quality parameters. Similar results were also observed in another mesocosm experiment with loricariid catfish (Hoover et al. 2013) and this may be due to the relatively small body size of sailfin catfishes used in both experiments. It has been reported that adult sailfin catfish can cause bank erosion, sedimentation and increased turbidity during the spawning season as they burrow into banks and bottom sediments to make nests (Hoover et al. 2014). The levels of physico-chemical parameters measured in the experimental ponds in this study are quite typical of those in many standing floodplain water bodies in Bangladesh (Chaki et al. 2014) meaning similar outcomes may be expected in those environments.

The presence of sailfin catfish in water bodies of Bangladesh may also pose an indirect threat to other fish predators such as aquatic birds whose conservation is already a concern (Galib et al. 2018). Loricariids, even large ones like *Pterygoplichthys*, may serve as food for birds like cormorant *Phalacrocorax* spp. (Ríos-Muñoz 2015) and therefore, their presence in the wild might benefit similar birds in Bangladesh. On the other hand, fish-eating birds capturing sailfin catfish may have difficulty in swallowing the catfish due to their spines and body armour, and could lead to death as has been recorded for pelicans *Pelecanus* spp. (Hoover et al. 2004).

This study showed a competitive relationship between non-native sailfin catfish and native fish species, with native carps disadvantaged in controlled earthen ponds where availability of space and food were limited. Therefore, in an open natural habitat where there is more space available to limit species interactions, the adverse effects of sailfin catfish on native carps may not be evident until the density of sailfin catfish reaches a certain level. Further study, to determine the trajectories of the ecological responses of sailfin catfish and native carp species in the natural environment, would be helpful.

5 CONCLUSION

This study suggests that the presence of non-native sailfin catfish in Bangladeshi floodplain ecosystems, even at relatively low densities, may have an adverse impact on native fish species, since in controlled conditions sailfin catfish can strongly impact growth and survival of several high-valued cyprinid species, especially midwater and bottom omnivores. The very high survival rate of sailfin catfish observed in these mesocosm studies, and increasing occurrence in the wild across Bangladesh, demonstrates that this non-native species can adapt to the local environment easily and their colonisation could be rapid. An increasing proportion of this fish in a water body may adversely affect the native fishes and ecosystem as well as the aquaculture production. The results of this study may also be expected to be applicable to many other inland waters in SE Asia because of similar climatic conditions. Future research should focus on the assessment of population density of sailfin catfish and their impacts in open waters in Bangladesh.

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Table 1: Changes in mean body mass and survival rate of the studied species in relation to varying density of non-native sailfin catfish, obtained through Linear Mixed-Effect Modelling.

Native fish species	**Growth**		**Survival**	
	***F* value**	***p* value**	***F* value**	***p* value**
Sailfin catfish	2.2	0.122	1	0.417
Catla catla	5.4	**<0.001**	1	0.445
Labeo rohita	81.2	**<0.001**	2	0.159
Cirrhinus cirrhosus	153.0	**<0.001**	13.0	**<0.001**

Statistically significant values are shown in bold.

Table 2: Differences in gut content across experimental groups for studied fish species.

Fish	**Algae**		**Macrophyte**		**Zooplankton**		**Macroinvertebrate**		**Detritus**		**Mud**	
	F	***p***	***F***	***p***	***F***	***p***	***F***	***p***	***F***	***p***	***F***	***p***
Catla catla	23.2	**<0.001**	11.3	**<0.001**	14.8	**<0.001**	11.8	**<0.001**	7.0	**0.004**	–	–
Labeo rohita	4.2	**0.024**	84.3	**<0.001**	–	–	13.5	**<0.001**	16.7	**<0.001**	29.1	**<0.001**
Cirrhinus cirrhosus	4.6	**0.017**	–	–	11.7	**<0.001**	25.9	**<0.001**	10.6	**<0.001**	42.5	**<0.001**
Sailfin catfish	1.17	0.354	0.78	0.487	–	–	10.2	**0.005**	0.44	0.656	2.7	0.125

Statistically significant values are shown in bold.

Figure captions

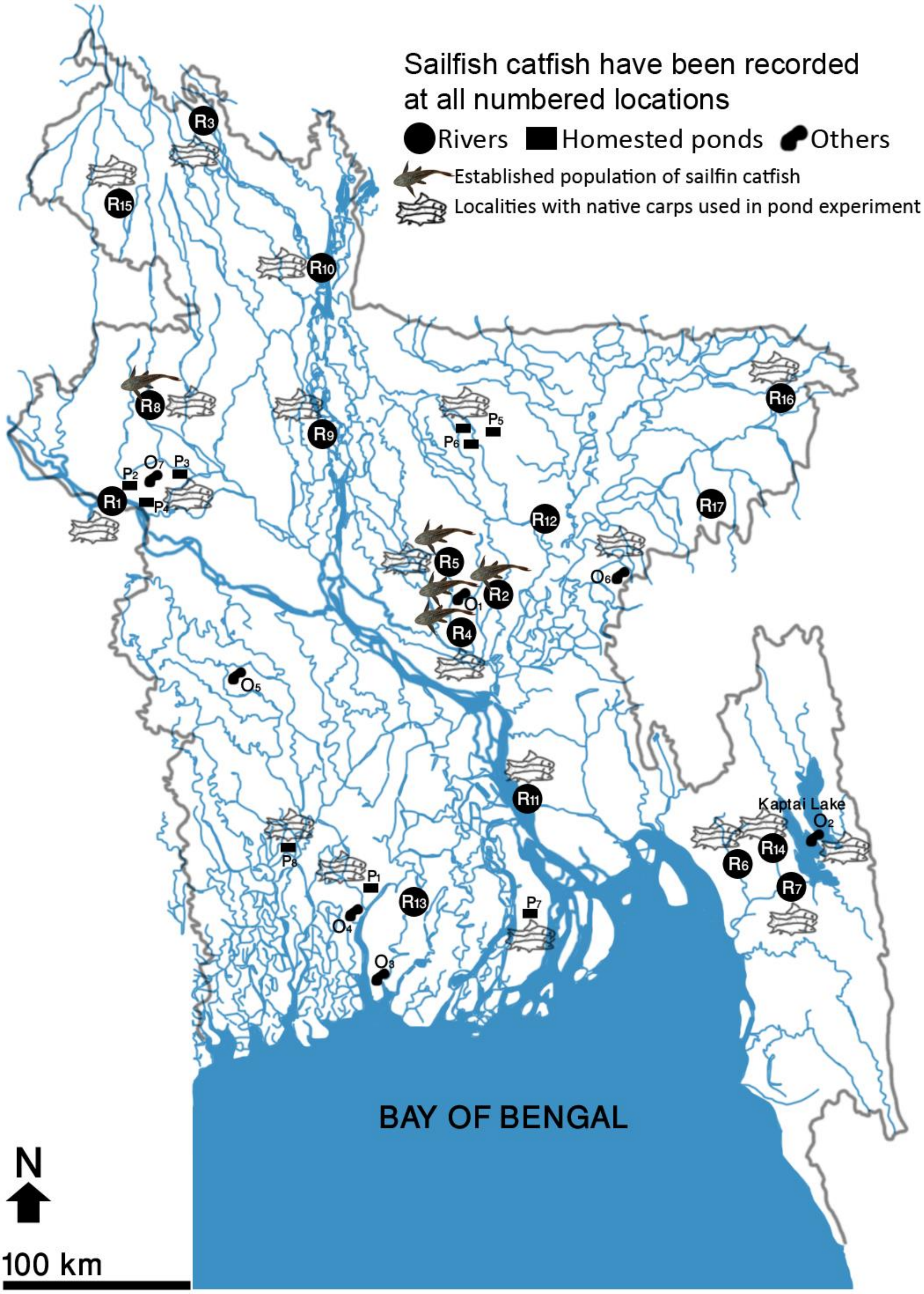

Figure 1: Map of Bangladesh showing distribution of sailfin catfish in various water bodies (all numbered water bodies have positive records of sailfin catfish).. Numbers in circular symbols represent river catchments: R_1, Padma River; R_2, Shitalakshya River; R_3, Teesta River; R_4, Buriganga River; R_5, Turag River; R_6, Halda River; R_7, Karnafuli River; R_8, Atrai River; R_9, Jamuna River; R_{10}, Brahmaputra River; R_{11}, Meghna River; R_{12}, Arial Kha River; R_{13}, Bishkhali River; R_{14}, Ichamati River; R_{15}, Punarbhaba River; R_{16}, Kushiyara River; R_{17}, Bilash River. For details of sailfin catfish at each numbered site, see Table S1.

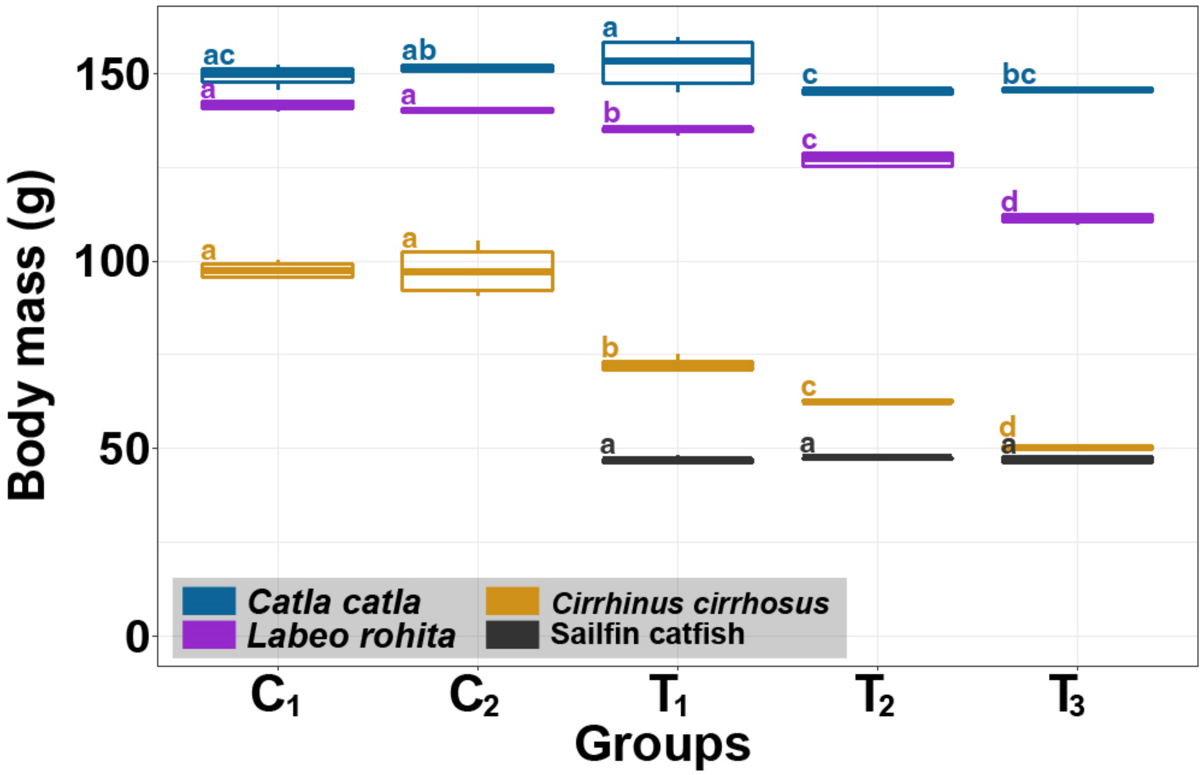

Figure 2: Boxplots showing final body mass of three native carp species and sailfin catfish in different experimental groups (C_1, native fish control; C_2, native fish biomass control; T_1, T_2 and T_3 are low-, medium- and high-sailfin catfish density treatment groups respectively). Midline within the box is the median; upper and lower limits of the box represent the third and first quartile (75th and 25th percentile) respectively. Different letters on the top of the boxplot represent significant difference between groups for each species.

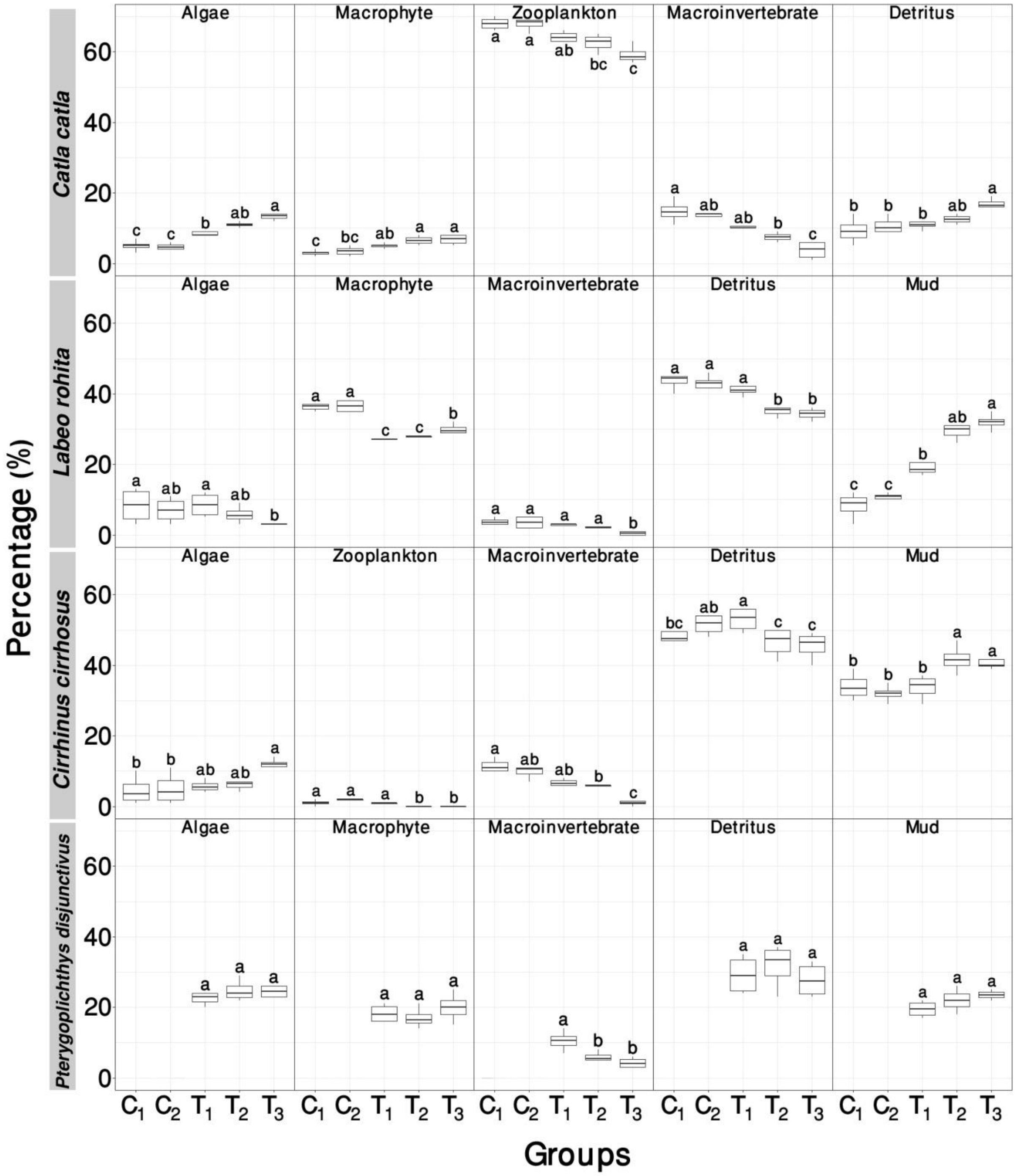

Figure 3: Food contents in the gut of native carp species and sailfin catfish across different experimental groups (C_1, native fish control; C_2, native fish biomass control; T_1, T_2 and T_3 are low-, medium- and high-density treatment groups respectively). Midline within the box is the median; upper and lower limits of the box represent the third and first quartile (75th and 25th percentile) respectively. Different letters above / below the boxplot represent significant difference between groups for each species.

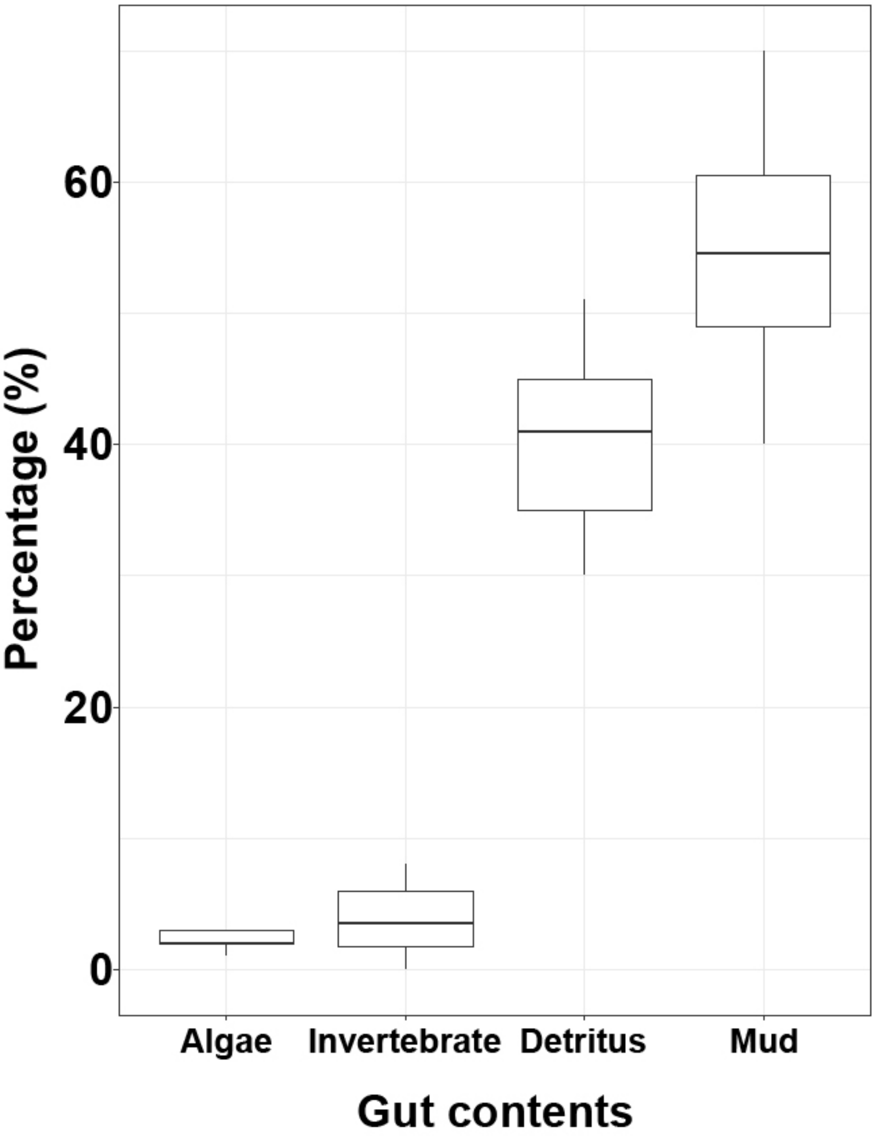

Figure 4: Gut contents of wild vermiculated sailfin crayfish from the Buriganga River showing dominance of organic detritus and mud in the diet. Midline within the box is the median; upper and lower limits of the box represent the third and first quartile (75th and 25th percentile) respectively.

SUPPLEMENTARY INFORMATION

Table S1: Occurrence records of sailfin catfish in Bangladesh. Species identification confirmation notes have been provided for cases where possible. All specimens, whose identification was possible by examining specimens or photographs, were identified as vermiculated sailfin catfish (*Pterygoplichthys disjunctivus*). Other records may be assumed to be the same species. Only one report (Hossain et al. 2018; Ref. 20 in data source) identified six specimens as Amazon sailfin catfish (*P. pardalis*). It was possible to re-examine the voucher specimens for two locations, out of three, and we identified these specimens as *P. disjunctivus*, based on markings on the ventral side (see the figure below, Figure S2). It was not possible to examine the third voucher specimen as it was no longer preserved at the reported place.

Serial number in Fig 1	Habitat and location	Introduction note	Remarks	Data source
Rivers				
R_1	Padma River, multiple location	Unknown	Two specimens (10 cm and 11.5 cm) first recorded in Aug 2021. Captured in small numbers by fishermen. Largest individual weighing 1 kg caught in Nov 2021. Confirmed as *P. disjunctivus*.	1–3
R_2	Shitalakshya River, Narayanganj	First recorded in 2018	Well-established through natural breeding. Confirmed as *P. disjunctivus*.	1, 4
R_3	Teesta River, Lalmonirhat	First recorded in 2022	Single specimen weighing 320 g was captured by a fisherman. Confirmed as *P. disjunctivus*.	5
R_4	Buriganga River, Dhaka	First recorded in 2017	Well-established through natural breeding. Believed to be introduced from nearby Gulshan Lake. Confirmed as *P. disjunctivus*.	1
R_5	Turag River, Gazipur and Dhaka	First recorded in 2018	Well-established through natural breeding. Believed to be introduced from Buriganga River. Confirmed as *P. disjunctivus*.	1, 6
R_6	Halda River, Chattogram	First recorded in 2021	Not abundant and captured in small amount by the fishermen.	6
R_7	Karnafuli River, Rangamati	First recorded in Jan 2022	One individual (approximately 160 mm) was captured by a fisherman.	7
R_8	Atrai River, Naogaon	First reported in 2014	Common in river. Largest individual caught was 1.25 kg. Confirmed as *P. disjunctivus*.	1, 8
R_9	Jamuna River, Bagura	First recorded in 2022	Not abundant and captured in small amount by the fishermen. Individual weighing 2 kg was captured.	9
R_{10}	Brahmaputra River, Gaibandha	First reported in 2015	Not abundant and captured in small amount by the fishermen. Confirmed as *P. disjunctivus*.	1, 10
R_{11}	Meghna River, Laxmipur	First recorded in 2022	One individual was captured by a fisherman in Feb 2022.	11
R_{12}	Arial Kha River, Kishoreganj	First recorded in 2021	One individual was captured by a fisherman in Nov 2021.	12
R_{13}	Bishkhali River, Borguna	Reported in 2022	Not abundant becoming common in recent times. Largest individual captured was 1050 g (Feb 2022).	13
R_{14}	Ichamoti River, Chattogram	Recorded in May 2018	Two individuals were captured by a fisherman.	14
R_{15}	Punarbhaba River, Dinajpur	Reported in 2019	Only occurrence of the species has been reported.	15
R_{16}	Kushiyara River, Sylhet	Reported in 2018	One individual was captured (~1.5 kg) by a fisherman	16
R_{17}	Bilash River, Moulvibazar	Reported in 2018	One individual was captured (~2 kg) by a fisherman	17
Homestead ponds				
P_1	Indurkani and Swarupkati, Pirojpur	Present since 2018.	25 individuals of different sizes were captured in Apr 2022. Nest (hole) in the pond embankment has been confirmed in several ponds. Confirmed as *P. disjunctivus*.	1, 18

P_2	Paba, Rajshahi	Recorded in Sep 2021	Two moderate-sized individuals (16 cm and 22 cm) along with >25 young (~6–7 cm) were captured by a pond owner. Confirmed as *P. disjunctivus*.	1
P_3	Durgapur, Rajshahi	Recorded in Jan 2022	One individual captured, about 30 cm in size. Confirmed as *P. disjunctivus*.	19
P_4	Charghat, Rajshahi	First recorded in Sep 2009.	Occurs in multiple ponds. Field survey confirmed presence of *P. disjunctivus*, not *P. pardalis* as reported by Hossain et al. (ref. 20).	1, 20
P_5	Gouripur, Mymensingh	Captured in Mar 2020; unknown source	One individual was captured and released into another pond.	21
P_6	Sadar, Mymensingh	First reported in Nov 2021.	Occur in multiple ponds. Two individuals (23.2 cm and 19.6 cm) were captured in May 2022 in one pond of the cantonment. Confirmed as *P. disjunctivus*.	1, 22
P_7	Lalmohon, Bhola	Occurs since 2015	Occurs in multiple ponds. 25 individuals were captured from one pond in Jan 2022. Confirmed as *P. disjunctivus*.	1, 23
P_8	Khulna	Captured in 2012	Two individuals were captured. Possibly *P. disjunctivus*.	20
Lakes, wetlands and others				
O_1	Gulshan Lake, Dhaka	Released by the aquarists when grown to a large size.	Well-established through natural breeding. Believed to be the first habitat outside captivity in the country. Confirmed as *P. disjunctivus*.	1
O_2	Kaptai Lake, Rangamati	First recorded in 2017	Not fully established, but occurs in fishermen's nets.	24–26
O_3	Local beel (wetland), Borguna	Captured in 2021	One individual was captured by a fisherman from local floodplain.	27
O_4	Local canal, Bagerhat	Captured in Sep 2021	One individual (about 1 kg in weight) was captured by a fisherman.	28
O_5	Local canal, Jhenaidaha	Captured in Mar 2021	One individual was captured by a fisherman.	29
O_6	Local beel, Brahmanbaria	Captured in Oct 2020	One individual weighing >500 g was captured by a fisherman.	30
O_7	Irrigation canal, Rajshahi	First captured in 2007	Multiple individuals were captured. Reported as *P. pardalis* by Hossain et al. (ref. 20) but could be misidentification. Possibly *P. disjunctivus*.	20

Data sources:

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30 https://www.daily-bangladesh.com/country/210332

Table S2: Post-hoc results showing variation in body mass and survival rate of the native fish species between experimental groups with or without vermiculated sailfin catfish. (C_1, native control without vermiculated sailfin catfish; C_2, native biomass control without vermiculated sailfin catfish; T_1, T_2 and T_3 are low, medium and high density treatment respectively).

Native fish species	**Growth**		**Survival**	
	***z* value**	***p* value**	***z* value**	***p* value**
Catla catla				
C_1 vs. C_2	–2.1	0.219	0.00	1.000
T_1 vs. C_1	0.3	0.998	0.00	1.000
T_2 vs. C_1	–1.5	0.541	–1.29	0.697
T_3 vs. C_1	–3.7	**0.002**	–1.29	0.697
T_1 vs. C_2	2.4	0.108	0.00	1.000
T_2 vs. C_2	0.6	0.979	–1.29	0.697
T_3 vs. C_2	–1.6	0.502	–1.29	0.697
T_3 vs. T_1	–4.0	**<0.001**	–1.29	0.697
T_2 vs. T_1	–1.9	0.341	–1.29	0.697
T_3 vs. T_2	–2.2	0.193	0.000	1.000
Labeo rohita				
C_1 vs. C_2	–0.2	0.998	0.00	1.000
T_1 vs. C_1	–3.8	**0.001**	0.00	1.000
T_2 vs. C_1	–9.5	**<0.001**	–1.19	0.797
T_3 vs. C_1	–14.8	**<0.001**	–2.24	0.166
T_1 vs. C_2	–3.6	**0.003**	0.000	1.000
T_2 vs. C_2	–9.3	**<0.001**	–1.1	0.797
T_3 vs. C_2	–14.5	**<0.001**	–2.2	0.166
T_3 vs. T_1	–10.9	**<0.001**	–2.2	0.166
T_2 vs. T_1	–5.7	**<0.001**	–1.7	0.797
T_3 vs. T_2	–5.2	**<0.001**	–1.1	0.797
Cirrhinus cirrhosus				
C_1 vs. C_2	0.2	0.998	0	1
T_1 vs. C_1	–8.5	**<0.001**	–1	0.856
T_2 vs. C_1	–13.9	**<0.001**	–3	**0.023**
T_3 vs. C_1	–20.1	**<0.001**	–6	**<0.001**
T_1 vs. C_2	–8.3	**<0.001**	–1	0.856
T_2 vs. C_2	–13.7	**<0.001**	–3	0.223
T_3 vs. C_2	–19.9	**<0.001**	–6	**<0.001**
T_3 vs. T_1	–11.6	**<0.001**	–5	**<0.001**
T_2 vs. T_1	–5.4	**<0.001**	–2	0.266
T_3 vs. T_2	–6.2	**<0.001**	–3	**0.023**

Statistically significant values are shown in bold.

Table S3: Gut contents of *Catla catla* across different experimental groups (C_1, native control without vermiculated sailfin catfish; C_2, native biomass control without vermiculated sailfin catfish; T_1, T_2 and T_3 are low, medium and high density treatment respectively), obtained through Linear Mixed-Effects Modelling.

Comparison	**Algae**		**Macrophyte**		**Zooplankton**		**Macroinvertebrate**		**Detritus**	
	z	***p***	***z***	***p***	***z***	***p***	***z***	***p***	***z***	***p***
C_2 vs. C_1	–0.19	0.997	0.80	0.931	–0.17	0.999	–0.40	0.995	1.45	0.594
T_1 vs. C_1	4.29	**<0.001**	3.26	0.009	–2.66	0.061	–1.37	0.647	1.83	0.357
T_2 vs. C_1	5.87	**<0.001**	4.99	<0.001	–3.97	**<0.001**	–2.77	**0.044**	2.69	0.056
T_3 vs. C_1	7.27	**<0.001**	5.22	<0.001	–6.48	**<0.001**	–6.00	**<0.001**	5.07	**<0.001**
T_1 vs. C_2	4.48	**<0.001**	2.47	0.099	–2.48	0.095	–0.97	0.870	0.38	0.996
T_2 vs. C_2	6.06	**<0.001**	4.19	<0.001	–3.80	**0.001**	–2.37	0.123	1.24	0.730
T_3 vs. C_2	7.46	**<0.001**	4.42	<0.001	–6.30	**<0.001**	–5.61	**<0.001**	3.62	**0.003**
T_2 vs. T_1	1.58	0.510	1.72	0.420	–1.32	0.681	–1.40	0.623	0.86	0.911
T_3 vs. T_1	2.98	**0.024**	1.96	0.288	–3.82	**0.001**	–4.64	**<0.001**	3.25	**0.010**
T_3 vs. T_2	1.40	0.628	0.23	0.999	–2.50	0.090	–3.24	**0.011**	2.39	0.119

Statistically significant values are shown in bold.

Table S4: Gut content of *Labeo rohita* across different experimental groups (C_1, native control without vermiculated sailfin catfish; C_2, native biomass control without vermiculated sailfin catfish; T_1, T_2 and T_3 are low, medium and high density treatment respectively), obtained through Linear Mixed-Effects Modelling.

Comparison	**Algae**		**Macrophyte**		**Macroinvertebrate**		**Detritus**		**Mud**	
	z	***p***	***z***	***p***	***z***	***p***	***z***	***p***	***z***	***p***
C_2 vs. C_1	–0.51	0.986	0.29	0.998	–0.54	0.984	–0.620	0.972	1.89	0.321
T_1 vs. C_1	0.50	0.987	–13.1	**<0.001**	–1.25	0.724	–1.061	0.827	5.65	**<0.001**
T_2 vs. C_1	–1.18	0.765	–12.2	**<0.001**	–2.03	0.252	–5.498	**<0.001**	8.11	**<0.001**
T_3 vs. C_1	–3.22	**0.011**	–8.70	**<0.001**	–6.51	**<0.001**	–6.053	**<0.001**	8.67	**<0.001**
T_1 vs. C_2	1.01	0.850	–13.3	**<0.001**	–0.71	0.954	–0.440	0.992	3.76	**0.002**
T_2 vs. C_2	–0.66	0.964	–12.5	**<0.001**	–1.50	0.566	–4.878	**<0.001**	6.22	**<0.001**
T_3 vs. C_2	–2.71	0.053	–8.99	**<0.001**	–5.98	**<0.001**	–5.433	**<0.001**	6.78	**<0.001**
T_2 vs. T_1	–1.68	0.449	0.83	0.922	–0.78	0.936	–4.437	**<0.001**	2.46	0.100
T_3 vs. T_1	–3.72	**0.002**	4.36	**<0.001**	–5.27	**<0.001**	–4.993	**<0.001**	3.02	**0.022**
T_3 vs. T_2	–2.04	0.246	3.53	**0.004**	–4.48	**<0.001**	–0.555	0.981	0.56	0.981

Statistically significant values are shown in bold.

Table S5: Gut contents of *Cirrhinus cirrhosus* across different experimental groups (C_1, native control without vermiculated sailfin catfish; C_2, native biomass control without vermiculated sailfin catfish; T_1, T_2 and T_3 are low, medium and high density treatment respectively), obtained through Linear Mixed-Effects Modelling.

Comparison	**Algae**		**Zooplankton**		**Macroinvertebrate**		**Detritus**		**Mud**	
	z	***p***	***z***	***p***	***z***	***p***	***z***	***p***	***z***	***p***
C_2 vs. C_1	0.22	0.999	2.12	0.210	–0.78	0.937	1.76	0.400	–2.12	0.210
T_1 vs. C_1	1.43	0.606	–0.57	0.979	–2.37	0.122	2.74	**0.048**	–0.25	0.999
T_2 vs. C_1	1.59	0.505	–3.51	**0.004**	–3.05	**0.020**	–1.89	0.324	7.59	**<0.001**
T_3 vs. C_1	3.81	**0.001**	–3.51	**0.004**	–9.12	**<0.001**	–2.64	0.064	7.40	**<0.001**
T_1 vs. C_2	1.21	0.745	–2.69	0.055	–1.60	0.499	0.99	0.860	1.87	0.333
T_2 vs. C_2	1.37	0.648	–5.53	**<0.001**	–2.27	0.155	–3.64	**0.002**	9.71	**<0.001**
T_3 vs. C_2	3.59	**0.003**	–5.63	**<0.001**	–8.34	**<0.001**	–4.39	**<0.001**	9.52	**<0.001**
T_2 vs. T_1	0.16	0.999	–2.93	**0.028**	–0.67	0.962	–4.64	**<0.001**	7.84	**<0.001**
T_3 vs. T_1	2.38	0.120	–2.93	**0.028**	–6.74	**<0.001**	–5.38	**<0.001**	7.65	**<0.001**
T_3 vs. T_2	2.23	0.170	0.00	1.00	–6.07	**<0.001**	–0.75	0.945	–0.19	1.000

Statistically significant values are shown in bold.

Table S6: Gut contents of vermiculated sailfin catfish across different treatment groups (T_1, T_2 and T_3 are low, medium and high-density treatment respectively), obtained through Linear Mixed-Effects Modelling.

Comparison	**Algae**		**Macrophyte**		**Macroinvertebrate**		**Detritus**		**Mud**	
	z	***p***	***z***	***p***	***z***	***p***	***z***	***p***	***z***	***p***
T_2 vs. T_1	NS		NS		–2.76	**0.016**	NS		NS	
T_3 vs. T_1	NS		NS		–4.49	**<0.001**	NS		NS	
T_3 vs. T_2	NS		NS		–1.73	0.195	NS		NS	

NS, not significant; statistically significant values are shown in bold.

Figure S1. Ventral marks of sailfin catfish found in aquatic habitats of Bangladesh confirms the identity as *Pterygoplichthys disjunctivus*.

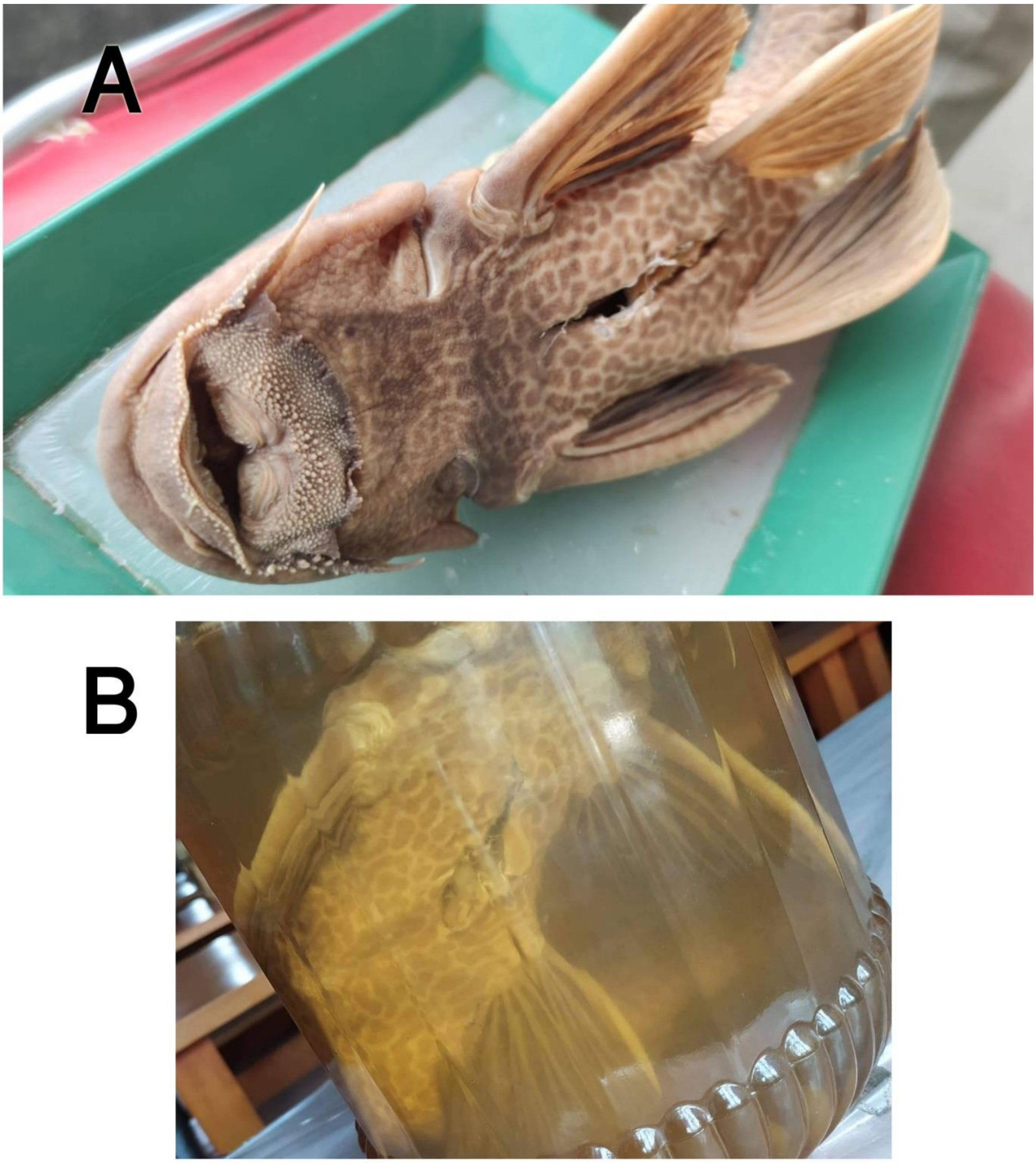

Figure S2: Two voucher specimens preserved at Zoology Laboratory of Kahalu Degree College (A; 48.6 cm total length) and Saiyad Ahmed College (B; ~60 cm total length) in Bogra, Bangladesh and identified as *Pterygoplichthys pardalis* by Hossain et al. 2018. Based on identification keys, characteristics and photographs (Hoover et al., 2014; Page & Robins, 2006), these specimens appeared to be *P. disjunctivus*. It was not possible to examine the third voucher specimen (16.4 cm, juvenile; photographed in Hossain et al. 2018) at the University of Rajshahi as it was no longer preserved.

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